Optimum Seral Stage for Northern Bobwhites as Influenced by Site Productivity
Author(s): Gary S. Spears, Fred S. Guthery, Steven M. Rice, Stephen J. Demaso, Bob Zaiglin
Reviewed work(s):
Source: *The Journal of Wildlife Management,* Vol. 57, No. 4 (Oct., 1993), pp. 805–811
Published by: Allen Press
Stable URL: http://www.jstor.org/stable/3809083
Accessed: 05/12/2011 19:05

OPTIMUM SERAL STAGE FOR NORTHERN BOBWHITES AS INFLUENCED BY SITE PRODUCTIVITY

GARY S. SPEARS,[1] Caesar Kleberg Wildlife Research Institute, Texas A&I University, Kingsville, TX 78363
FRED S. GUTHERY, Caesar Kleberg Wildlife Research Institute, Texas A&I University, Kingsville, TX 78363
STEVEN M. RICE,[2] Caesar Kleberg Wildlife Research Institute, Texas A&I University, Kingsville, TX 78363
STEPHEN J. DEMASO,[3] Caesar Kleberg Wildlife Research Institute, Texas A&I University, Kingsville, TX 78363
BOB ZAIGLIN, Piloncillo Ranch, Uvalde, TX 78801

Abstract: According to theory, maximum populations of a species occur within the stage of ecological succession to which the species is adapted. The maximizing seral stage may differ among areas, which illustrates a need for understanding factors that regulate the relationship. Thus, we tested the hypothesis that optimum seral stage for northern bobwhites (*Colinus virginianus*) on southern rangeland varies inversely with site productivity. Data were collected on 6 sites (2 each in early, mid-, and late seral status) in each of 3 regions of different productivity (potential annual herbaceous biomass production) in the Rio Grande Plains and Gulf Coast Prairies of Texas during 1989–90. Results supported a predicted interaction; on more productive sites, bobwhite density was highest with early seral status, whereas on less productive sites, density was unaffected by seral status. Contrary to a prediction, bobwhite density did not increase with seral stage on less productive sites. Results did not refute the predicted existence of commonalities (i.e., habitat features with similar values in dissimilar seral stages on sites of different productivity). Our data suggest that site productivity is 1 factor that may help managers identify the correct seral stage in habitat management decisions.

A basic theory of wildlife habitat management is that animal species are adapted to certain stages of ecological succession, and that provision of the correct successional stage will maximize population density (Bailey 1984:225, Robinson and Bolen 1984:28, Patton 1992:31). Animals have been classified as climax, developmental, or mixed-stage species, depending upon their successional affiliations, and management has proceeded accordingly.

Bailey (1984:228) recognized that an animal might be adapted to different successional stages in different geographic zones. This circumstance does not invalidate the general theory, but argues against its dogmatic application in habitat management decisions. The circumstance also highlights the need for understanding of processes that alter an animal's successional affiliation as location changes.

Northern bobwhites inhabiting semiarid rangeland show inconsistent relationships between abundance and seral stage as reflected in range condition class (we use the terms "range condition class" [Dyksterhuis 1949] and "seral stage" interchangeably after Pieper and Beck [1990]). During drought in the western Rio Grande Plains of Texas, sites in higher range condition (more perennial grass cover) had higher densities of bobwhites than sites in lower range condition (Campbell-Kissock et al. 1984). Bobwhite numbers were positively correlated with canopy coverage and biomass of grasses. Fair to good range condition was thought to benefit bobwhites because of a more diverse and stable food supply in comparison with poor range condition (Campbell-Kissock et al. 1985).

Conversely, in the eastern Rio Grande Plains, vegetation attributes reflecting lower range condition classes were found to benefit bobwhites. These attributes included greater coverage by bare ground and forbs and lesser coverage by grasses (Hammerquist-Wilson and Crawford 1981, Wilkins 1987, Schulz and Guthery 1988). Diet quality of bobwhite chicks was higher in pastures in poor range condition than in those in good range condition (Weaver 1984). The goals of good range condition and high bobwhite density appear incompatible in those portions of the Rio Grande Plains with high vegetation productivity (T. B. Doerr and N. L. Silvy, Tex. A&M Univ., unpubl. rep.).

The above results conflict because higher range condition and more grass benefitted bobwhites

[1] Present address: 2941 Little River Road, Madison, GA 30650.
[2] Present address: Land Planning Group, Mount Dora, FL 32757.
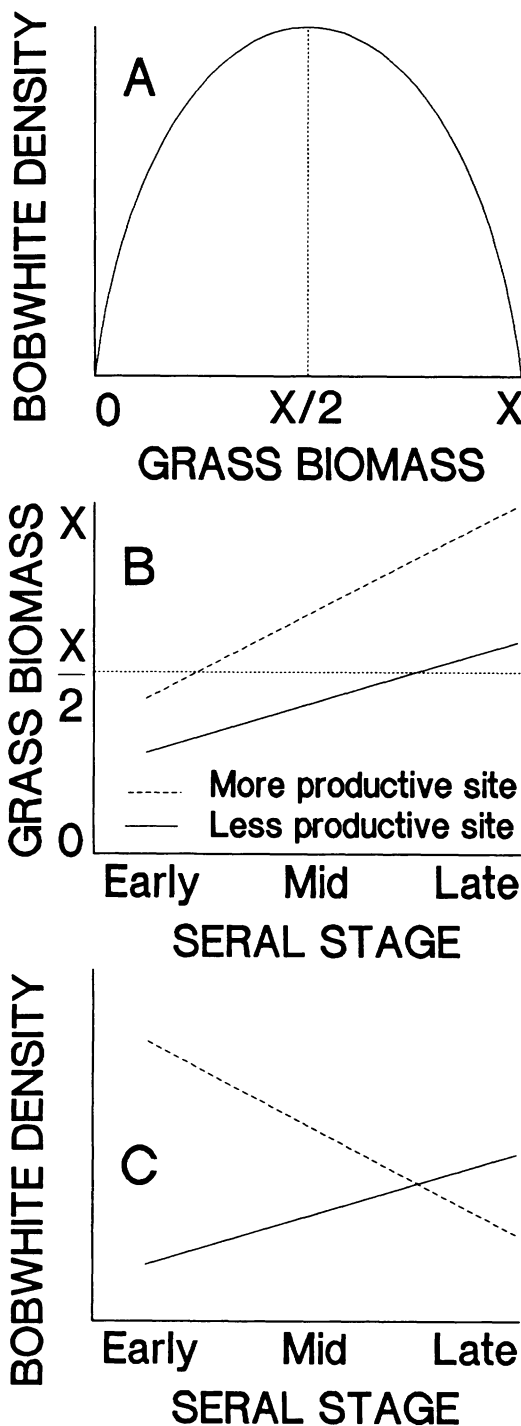[3] Present address: Oklahoma Department of Wildlife Conservation, Oklahoma City, OK 73105.

Fig. 1. Theoretical construct for the hypothesis that optimum seral stage for northern bobwhites varies inversely with site productivity. A. Hypothesized relationship between bobwhite abundance and grass biomass. B. Relationship between grass biomass and seral stage on sites of different vegetation productivity. C. Predicted interaction effect between bobwhite abundance and seral stage on sites of different productivity.

in the western Rio Grande Plains, whereas lower range condition and less grass benefitted these birds in the eastern Rio Grande Plains. These regions differ markedly in potential annual herbaceous biomass production (productivity). Soil fertility, frost-free period, and precipitation are primary mediators of vegetation productivity on semiarid rangeland. Productivity may regulate the response of quail to seral stage, but this assertion compels a theoretical construct.

Given constancy in other variables (disease, predation, harvest, special habitat requirements), bobwhite abundance may vary in a paraboloid manner with grass biomass (dry mass per unit area) (Fig. 1A), a key feature of seral stage on rangeland (Dyksterhuis 1949). This relationship portrays the empirical observation (e.g., Schroeder 1985) that there can be too little, an optimum amount, or too much grass in bobwhite habitat. The relationship implies that bobwhite density is positively correlated with grass biomass in a certain domain (range of x values) and negatively correlated in another domain. In general, grass biomass is expected to increase with seral stage; however, absolute amounts will be higher on more productive than on less productive sites, given a seral stage and constancy in other conditions (grazing pressure, environmental stochasticity, etc.) (Fig. 1B). If a site of low productivity had seral stages that encompassed the domain of positive correlation, then bobwhite abundance would bear a positive relationship to seral stage on this site. The converse would be true on a site of high productivity.

The above arguments lead to the hypothesis that optimum seral stage for northern bobwhites varies inversely with site productivity on southern rangeland. A prediction of the hypothesis is an interaction effect between bobwhite abundance and seral stage on sites of different productivity (Fig. 1C). Because bobwhite adaptations are largely fixed, a corollary prediction is the existence of habitat commonalities. We define commonalities as habitat features with similar values on dissimilar seral stages on sites of different productivity (e.g., the horizontal line in Fig. 1B intersects the grass biomass lines at a common value in different seral stages). Our purpose was to test the hypothesis by testing the predictions.

(Contrib. No. 401) provided financial and logistical support. E. C. Hellgren, R. L. Bingham, T. E. Fulbright, and D. L. Drawe commented on an early draft of the manuscript. The Animal Care and Use Committee, Texas A&I University, reviewed and approved this study before field sampling began.

STUDY AREAS AND METHODS

We collected data in 3 regions of different productivity in southern Texas during 1989–90: Gulf Coast Prairies (high), Central Rio Grande Plains (medium), and Western Rio Grande Plains (low). During wetter years, annual production of herbaceous vegetation is estimated at 6,162, 5,602, and 4,929 kg/ha (air-dry mass), respectively, for climax communities in these regions (Spears 1991). We used seral stages corresponding to range condition classes (Dyksterhuis 1949) (poor = early seral, fair = mid seral, good = late seral) to classify site successional status (Pendleton 1989, Pieper and Beck 1990). In August 1989, U.S. Soil Conservation Service personnel and resident biologists determined range condition on pastures in which study sites would be located. Two sites for each seral stage were located randomly within pastures in each region (6 sites/region).

On each site, 4 800-m north–south line transects were established, beginning from a random point. Distance between transects was 300 m. Bobwhite densities were estimated seasonally from flushing observations along transects. Transects were walked by 3 observers in autumn 1989 (Sep–Oct), spring 1990 (Feb–Mar), and autumn 1990 (Sep–Oct). Counters followed recommendations of Guthery (1988) in collecting transect data. Each transect was walked 10 times, giving a sampling effort of 32 km/site per season.

Effective strip width $(2/\hat{f}(0))$ was estimated for each region and sampling period with the computer program TRANSECT (Burnham et al. 1980) (Table 1). We used the Fourier series detection model for ungrouped perpendicular distances, because of its model robustness, pooling robustness, efficiency, fit to the shape criterion, and performance with small samples (n = 30–40) (Burnham et al. 1980). Because spring samples (no. of perpendicular distance measurements) within regions were low (≤22), effective strip widths from autumn 1989 were used to estimate densities in spring 1990. Otherwise, we used region- and time-specific esti-

Table 1. Attributes of line transect data collected on northern bobwhites during autumn (Sep–Oct) in 3 regions of southern Texas, 1989–90.

Region Year	Covey size			Strip width[b]		
	n[a]	$\bar{x}$	SE	n	$\hat{f}(0)$	SE
Gulf Coast Prairies						
1989	53	6.9	0.60	39	0.0374	0.0046
1990	48	8.7	0.68	33	0.1269	0.1091
Cent. Rio Grande Plains						
1989	41	5.7	0.78	31	0.0781	0.0141
1990	21	6.1	0.91	16	0.1394	0.0162
West. Rio Grande Plains						
1989	80	7.2	0.40	36	0.0446	0.0147
1990	115	7.5	0.43	28	0.0578	0.0384

[a] Sample size exceeds that of strip width because of incidental counts on study sites.
[b] Effective strip width = $2/\hat{f}(0)$ in meters.

mates of effective strip widths on sites under the assumption that widths were similar ($P > 0.05$) among sites within regions and seasons.

Biomass of herbaceous vegetation was determined from 20 0.5- × 0.5-m quadrats/site (5 quadrats/800-m transect) in April and July 1990. Quadrats were located at 150-m intervals along the 800-m transects. Vegetation was clipped, separated by forbs and grasses, and oven-dried at 60–70 C to a constant mass.

Percent canopy coverage of grasses, forbs, litter, and bare ground was estimated following Daubenmire (1959). Forty 2- × 5-dm plots/site (9 plots/800-m transect and 1 plot between 800-m transects) were sampled in April and July 1990. Plots located 5 m east of 800-m transects were spaced at 100-m intervals.

We used means of dependent variables (quail density and habitat measurements) from sites in statistical analysis to obtain proper replication. A repeated (3 sampling periods) measures design was used to test for seral stage effects on mean bobwhite density within regions, whereas 1-way ANOVA's were used to determine seral stage effects on habitat variables within regions. We identified seral stages with different ($P < 0.05$) bobwhite densities and vegetation attributes with Tukey's test. The data were not amenable to testing for region and interaction effects in a 3 × 3 factorial model, because seral stages were not homologous among regions (composition and speciation of vegetation within seral stages differed among regions). The interaction was confirmed if bobwhite density differences among seral stages were not the same for each region (level of site productivity).
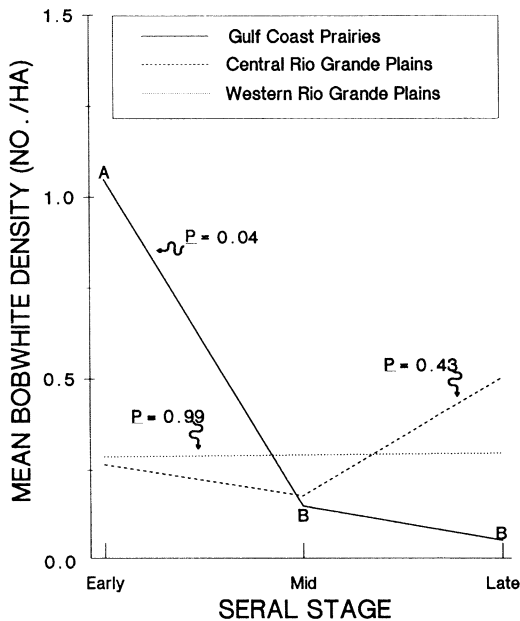
Fig. 2. Relationships between mean density of northern bob-whites and seral stages in regions of different vegetation productivity, southern Texas, 1990–91. Densities with different letters in the Gulf Coast Prairies differed (*P* < 0.05).

We used factor analysis (Afifi and Clark 1984: 330–360) to identify subsets of linearly intercorrelated vegetation and habitat variables and thereby reduce the dimensions of the data sets. Principal factor analysis with VARIMAX rota-

tion (SAS Inst. Inc. 1988:450–492) was performed on 17 spring and 15 summer response variables. Based on the factor patterns, known habitat requirements of bobwhites, and variables relevant to our research hypothesis, we selected 4 variables for presentation ($\bar{x}$ coverage [%] of herbaceous vegetation and litter, $\bar{x}$ exposure [%] of bare ground, and $\bar{x}$ dry mass [kg/ha] of herbaceous vegetation). Spears (1991) provided details on vegetation analyses.

RESULTS

Seral stage affected mean bobwhite density in the Gulf Coast Prairies, whereas no effects were observed in the central and western Rio Grande Plains (Fig. 2). Results were partially consistent with the research hypothesis (i.e., the early seral stage supported the highest bobwhite density in the most productive region). An interaction effect was observed, but it did not occur as hypothesized. Density did not increase with seral stage in less productive regions (cent. and west. Rio Grande Plains).

Seral stage affected ≥1 key habitat variable in each region at $P \leq 0.1$ (Fig. 3). Differences in habitat variables among seral stages were most pronounced in the Gulf Coast Prairies (most productive region) and least pronounced in the western Rio Grande Plains (least productive region). Habitat variables with high factor loadings (Table 2) in common with those presented

Table 2. Rotated factor pattern for selected vegetation and habitat variables on 18 sites in southern Texas, April and July 1991.

Time Variable[b]	Factor[a]			
	1	2	3	4
April[c]				
Live-standing forb coverage (%)	93	−24	−21	−12
Total-standing herbaceous vegetation coverage (%)	82	37	38	7
Forb biomass (kg/ha dry mass)	72	10	−2	−33
Live-standing perennial grass coverage (%)	10	91	30	−13
Grass biomass (kg/ha dry mass)	−12	84	−11	37
Herbaceous vegetation biomass (kg/ha dry mass)	41	83	−11	10
Litter coverage (%)	−7	−6	90	−17
July[d]				
Total standing herbaceous vegetation coverage (%)	86	19	35	−1
Herbaceous vegetation biomass (kg/ha dry mass)	84	43	−1	−22
Live-standing perennial grass coverage (%)	83	−32	32	19
Dead-standing forb coverage (%)	−21	89	−15	−7
Litter coverage (%)	12	84	15	1
Live-standing forb coverage (%)	36	−6	90	−6
Dead-standing grass coverage (%)	33	−31	−75	−10

[a] Factor loadings were multiplied by 100.
[b] Variables with high loadings within a factor were intercorrelated.
[c] Variables presented were selected from 17 variables analyzed.
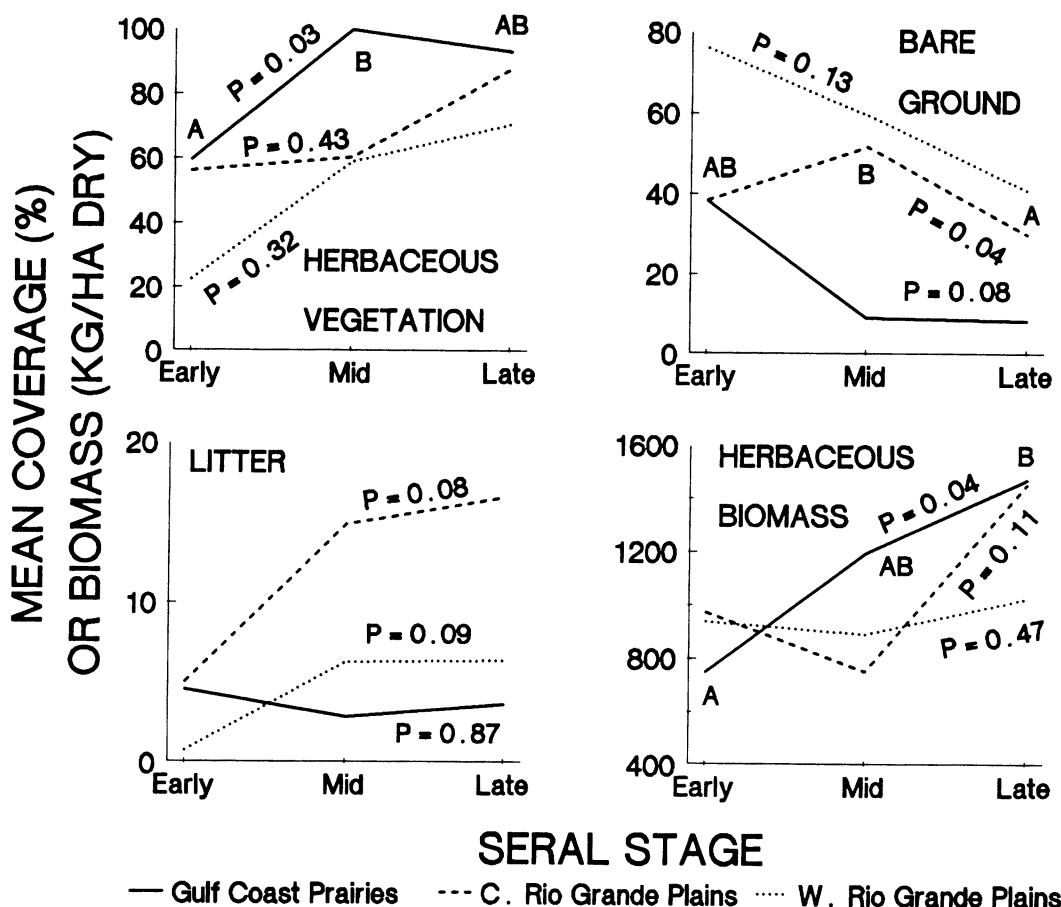[d] Variables presented were selected from 15 variables analyzed.

Fig. 3. Relationships between mean values for habitat variables and seral stages in regions of different vegetation productivity, southern Texas, 1990–91. Means with different letters in the same region differed ($P < 0.05$).

in Fig. 3 would show responses similar to those in Fig. 3. For example, a graph of forb biomass (loading = 72 on Factor 1) would appear similar to that of herbaceous vegetation coverage (loading = 82 on Factor 1).

Comparative values of habitat variables among seral stages within regions (Fig. 3) and among regions were generally consistent with expectations. Coverage by herbaceous vegetation and litter increased with seral stage, coverage by bare ground decreased, and biomass of herbaceous vegetation increased. Exceptions to these trends were observed (e.g., herbaceous vegetation and litter coverage in the Gulf Coast Prairies and bare ground and herbaceous biomass in the cent. Rio Grande Plains; Fig. 3). Comparative coverage values for herbaceous vegetation and bare ground were consistent with a portion of the theoretical construct (Fig. 1B,

but herbaceous biomass, which was correlated with perennial grass coverage (Table 2), was less supportive of the construct.

Confirming habitat commonalities was complicated by weak seral stage effects on habitat variables in two of 3 regions. This circumstance rendered moot the prediction of similar habitat values in dissimilar seral stages. If seral stage has no effect on a key habitat variable in a given region, then like values for the variable could occur in both similar and dissimilar seral stages among regions.

Bare ground was the most useful variable for testing the prediction of commonalities, because of relatively strong seral stage effects ($P \leq 0.13$) in each region (Fig. 3). Coverage by bare ground averaged 38.5 ± 10.0% (SE) in early seral stages in the Gulf Coast Prairies versus 41.1 ± 1.6% in late seral stages in the western Rio Grande

Plains. Also, respective regional values for mean coverage of herbaceous vegetation were 59.8 ± 3.3% and 70.7 ± 11.5%. These results were consistent with the predicted existence of habitat commonalities.

DISCUSSION

Our use of the Dyksterhuis (1949) system of range condition classification raises certain issues concerning ecological succession on rangelands relative to the hypothesis tested. The Dyksterhuis system has fallen into disfavor for semantic (Smith 1989) and ecological reasons. Rangeland vegetation can enter stable states wherein succession is arrested (Friedel 1991, Laycock 1991). Also, the Dyksterhius system is deterministic by construction and application, whereas ecological succession on rangeland may be stochastic (Westoby et al. 1989). With stochasticity the outcomes of succession cannot be predicted. Stable states render our hypothesis moot, except to the extent that management can alter standing biomass of herbaceous vegetation within a stable state. Stochasticity in succession does not necessarily affect our hypothesis if seral stages on different sites reflect circumstances similar to those portrayed in Figure 1B.

Because of erratic precipitation in southern Texas (Norwine and Bingham 1986) and the powerful influence of precipitation on vegetation and bobwhite population dynamics in this region (Lehmann 1953, Kiel 1976, Rice et al. 1993), our results must be considered in the context of weather before and during data collection. Droughty conditions, which reduce bobwhite reproduction, prevailed on our study areas during 1988–89 (Rice 1991). Precipitation during October 1989–September 1990 was >2 times that of the same period in the preceding year, and for the calendar year precipitation was approximately average in 1990. Drought preceding and during data collection probably reduced and equalized quail densities at low levels across seral stages in the central and western Rio Grande Plains. The expectation is for declining (nonreproducing) quail populations to converge to the same density as time passes.

Moreover, drought probably reduced variation in habitat variables (e.g., bare ground exposure) among seral stages within regions by effects on vegetation production. The effects of drought were less pronounced in the Gulf Coast Prairies than in the Rio Grande Plains, because the Coastal Prairies received about twice as much

effective precipitation during 1988–90 (Rice 1991).

Precipitation effects illustrate that our hypothesis has stochastic underpinnings, which imply that it relates specifically to average densities, given seral stage and site productivity. The variability imposed by weather may be exacerbated by other ecological processes. For example, as habitat quality declines, annual variation in population size may increase (e.g., O'Connor 1986). Such variability is a corollary of density-dependent habitat selection (Krohn 1992). In the context of our hypothesis, population variability imposed by density-dependent habitat selection should track average population size as mediated by seral stage and site productivity.

MANAGEMENT IMPLICATIONS

Whereas our results were inconsistent with elements of the research hypothesis, especially the concept that bobwhite density increases with seral stage on less productive sites, the inconsistencies may have accrued because of unique weather conditions during data collection and the stochastic nature of the hypothesis. Moreover, previous research has shown a positive relationship between bobwhite density and seral stage on less productive sites during drought (Campbell-Kissock et al. 1984). We observe, also, that bobwhites are relatively constant in size and physical abilities, and that this constancy implies a certain constancy in vegetation structure to which the bird is adapted. This more or less constant structure would be expected to prevail in different seral stages according to site productivity (Fig. 1B). Therefore, the research hypothesis remains tenable, and we conclude that site productivity, when considered against the backdrop of adaptation, is useful in identifying optimum seral stage for bobwhites and perhaps for other ground-dwelling species sympatric with bobwhites.

The hypothesis has direct implications on management philosophy. Management of successional status has long been recognized as the most powerful approach to bobwhite management (Ellis et al. 1969). Traditional knowledge holds that the bobwhite is a lower successional species (Rosene 1969:11–15). Our hypothesis indicates the bobwhite should be considered a mid- to late successional species on less productive sites, where the correct management posture may be protective rather than aggressive.

LITERATURE CITED

AFIFI, A. A., AND V. CLARK. 1984. Computer-aided multivariate analysis. Wadsworth, Inc., Belmont, Calif. 458pp.

BAILEY, J. A. 1984. Principles of wildlife management. John Wiley & Sons, New York, N.Y. 373pp.

BURNHAM, K. P., D. R. ANDERSON, AND J. L. LAAKE. 1980. Estimation of density from line transect sampling of biological populations. Wildl. Monogr. 72:202pp.

CAMPBELL-KISSOCK, L., L. H. BLANKENSHIP, AND L. D. WHITE. 1984. Grazing management impacts on quail during drought in the northern Rio Grande Plains, Texas. J. Range Manage. 37: 442–446.

———, ———, AND J. W. STEWART. 1985. Plant and animal foods of bobwhite and scaled quail in southwest Texas. Southwest. Nat. 30:543–553.

DAUBENMIRE, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Sci. 33:43–64.

DYKSTERHUIS, E. J. 1949. Condition and management of rangeland based on quantitative ecology. J. Range Manage. 2:104–115.

ELLIS, J. A., W. R. EDWARDS, AND K. P. THOMAS. 1969. Responses of bobwhites to management in Illinois. J. Wildl. Manage. 33:749–762.

FRIEDEL, M. H. 1991. Range condition assessment and the concept of thresholds: a viewpoint. J. Range Manage. 44:422–426.

GUTHERY, F. S. 1988. Line transect sampling of bobwhite density on rangeland: evaluation and recommendations. Wildl. Soc. Bull. 16:193–203.

HAMMERQUIST-WILSON, M. M., AND J. A. CRAWFORD. 1981. Response of bobwhites to cover changes within three grazing systems. J. Range Manage. 34:213–215.

KIEL, W. H., JR. 1976. Bobwhite quail population characteristics and management implications in south Texas. Trans. North Am. Wildl. and Nat. Resour. Conf. 41:407–420.

KROHN, W. R. 1992. Sequence of habitat occupancy and abandonment: potential standards for testing habitat models. Wildl. Soc. Bull. 20:411–444.

LAYCOCK, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. J. Range Manage. 44:427–433.

LEHMANN, V. W. 1953. Bobwhite population fluctuations and vitamin A. Trans. North Am. Wildl. Conf. 18:199–246.

NORWINE, J., AND R. BINGHAM. 1986. Frequency and severity of drought in south Texas: 1900–1983. Pages 1–17 *in* R. D. Brown, ed. Livestock and wildlife management during drought. Caesar Kleberg Wildl. Res. Inst., Texas A&I Univ., Kingsville.

O'CONNOR, R. J. 1986. Dynamical aspects of avian habitat use. Pages 235–240 *in* J. Verner, M. L. Morrison, and C. J. Ralph, eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison.

PATTON, D. R. 1992. Wildlife habitat relationships in forested ecosystems. Timber Press, Portland, Oreg. 392pp.

PIEPER, R. D., AND R. F. BECK. 1990. Range condition from an ecological perspective: modifications to recognize multiple use objectives. J. Range Manage. 43:550–552.

PENDLETON, D. T. 1989. Range condition as used in the Soil Conservation Service. Pages 17–34 *in* W. K. Lauenroth and W. A. Laycock, eds. Secondary succession and the evaluation of rangeland condition. Westview Press, Boulder, Colo.

RICE, S. M. 1991. Models for estimating bobwhite habitat quality on subtropical, subhumid rangeland. M.S. Thesis, Texas A&I Univ., Kingsville. 66pp.

———, F. S. GUTHERY, G. S. SPEARS, AND S. J. DEMASO. 1993. A precipitation-habitat model for northern bobwhites on semiarid rangeland. J. Wildl. Manage. 57:92–102.

ROBINSON, W. L., AND E. G. BOLEN. 1984. Wildlife ecology and management. Macmillan Publ. Co., New York, N.Y. 478pp.

ROSENE, W. 1969. The bobwhite quail: its life and management. Rutgers Univ. Press, New Brunswick, N.J. 418pp.

SAS INSTITUTE INC. 1988. SAS/STAT user's guide, release 6.03 ed. SAS Inst. Inc., Cary, N.C. 1028pp.

SCHROEDER, R. L. 1985. Habitat suitability models: northern bobwhite. Biol. Rep. 82 (10.104). U.S. Fish and Wildl. Serv., Washington, D.C. 32pp.

SCHULZ, P. A., AND F. S. GUTHERY. 1988. Effects of short duration grazing on northern bobwhites: a pilot study. Wildl. Soc. Bull. 16:18–24.

SMITH, E. L. 1989. Range condition and secondary succession: a critique. Pages 103–141 *in* W. K. Lauenroth and W. A. Laycock, eds. Secondary succession and the evaluation of rangeland condition. Westview Press, Boulder, Colo.

SPEARS, G. S. 1991. Optimum seral stage for northern bobwhites as influenced by site productivity. M.S. Thesis, Texas A&I Univ., Kingsville. 89pp.

WEAVER, L. J. 1984. Food habits of adopted bobwhite quail chicks in south Texas. M.S. Thesis, Texas A&I Univ., Kingsville. 92pp.

WESTOBY, M., B. WALKER, AND I. NOY-MEIR. 1989. Opportunistic management for rangelands not at equilibrium. J. Range Manage. 42:266–274.

WILKINS, R. N. 1987. Influence of grazing management on population attributes, habitats, and habitat selection of bobwhites in south Texas. M.S. Thesis, Texas A&M Univ., College Station. 79pp.