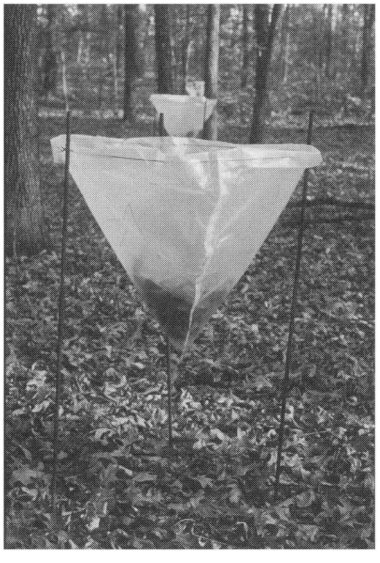
Tests of wildlife habitat models to evaluate oak-mast production

Richard L. Schroeder and Larry D. Vangilder

Abstract We measured oak-mast production and forest structure and composition in the Ozark Mountains of Missouri and tested the accuracy of oak-mast prediction variables from 5 Habitat Suitability Index (HSI) species models. Acorn production was positively associated with several measures of abundance and canopy cover of oak trees, and with an index of mast production for all 5 HSI models. We developed 2 modified oak-mast models, based on inputs related to either oak tree density or oak canopy cover and diversity of oak tree species. The revised models accounted for 22–32% of the variance associated with acorn abundance. Future tests of HSI models should consider: (1) the concept of upper limits imposed by habitat and the effects of nonhabitat factors; (2) the benefits of a top-down approach to model development; and (3) testing models across broad geographic regions.

Key words acorn, habitat, mast, model, oak, *Quercus* spp., wildlife

The importance of oak (*Quercus* spp.) mast as food for a variety of wildlife species has been well documented (Martin et al. 1961, Goodrum et al. 1971, Shaw 1971). Mast production is a function of the age and size of trees, inherent tree characteristics, canopy cover, stem density, competition, and climate (Goodrum et al. 1971). Field biologists need methods to predict forest mast production and to know which forest attributes to manage to increase mast production (McGee 1989). Forest managers cannot alter inherent tree characteristics or weather, but they often can change forest structure and composition. Most previous studies of oak-mast production (Downs and McQuilkin 1944, Cypert 1951, Harlow and Eikum 1963, Goodrum et al. 1971, Christisen and Kearby 1984) estimated acorn numbers or biomass for individual trees and were not useful in assessing conditions for entire stands. Although some studies (Minckler and McDermott 1960, Beck 1977) measured acorn production for entire stands, they did not provide comprehensive forest stand data. Thus, these studies cannot be used to predict forest mast production in other stands.



Close up view of acorn trap.

The U.S. Fish and Wildlife Service Habitat Suitability Index (HSI) model series (Schamberger et al. 1982) includes models for the mallard (*Anas platyrhynchos*; Allen 1987*b*), eastern wild turkey (*Meleagris gallopavo sylvestris*; Schroeder 1985*b*), northern bobwhite (*Colinus virginianus*; Schroeder 1985*a*), gray squirrel (*Sciurus carolinensis*; Allen 1987*a*), and fox squirrel (*Sciurus niger*; Allen 1982). Each HSI model includes variables that predict potential mast production based on forest stand conditions. The rating scale for each variable

Address for Richard L. Schroeder: U.S. Geological Survey, Biological Resources Division, Midcontinent Ecological Science Center, 4512 McMurry Avenue, Fort Collins, CO 80525–3400, USA. Address for Larry D. Vangilder: Missouri Department of Conservation, Fish and Wildlife Research Center, 1110 South College Avenue, Columbia, MO 65201, USA.

is a Suitability Index (SI) ranging from 0 (conditions unsuitable for mast production) to 1.0 (conditions suitable for maximum mast production; Fig. 1). SI values for ≥1 variables are used to produce an overall index of potential acorn production. These models were developed from a review and synthesis of existing qualitative and quantitative studies and reviews by species experts. The hypotheses in the models were not tested prior to model publication. To test the acorn prediction variables in these 5 HSI models, we conducted a 5-year study of oak-mast production in the Missouri Ozark Region. Our objectives were to determine the relationship between composition and structure of forest stands and oak-mast production, to test the mast variables presented in the 5 HSI models using systematically collected acorn data, and to determine the feasibility of producing a single improved mast-prediction model.

Study area and methods

This study was conducted on 2 areas in the Missouri Ozark Mountains. The South Study Area (SSA) is in the Eleven Point Ranger District of the Mark Twain National Forest in Shannon, Oregon, and Carter counties. More than 90% of the area is managed by the U.S. Forest Service. The Peck Ranch Conservation Area (PRCA) is in northwest Carter County and is managed by the Missouri Department of Conservation. We selected lands for sampling that were dominated by oak forest, including 18,098 ha on the SSA and 7,698 ha on the PRCA. Each study area was stratified into 4 Ecological Land Types (ELT; Miller 1981): hollow bottoms (ELTs 1-6), ridge tops (ELTs 7, 11), south- and west-facing slopes (ELTs 17, 19, 21, 22, 23), and north- and east-facing slopes (ELTs 18, 20). We randomly selected 5 0.2-ha plots (38.5 x 52 m) in each ELT in each study area for sam-

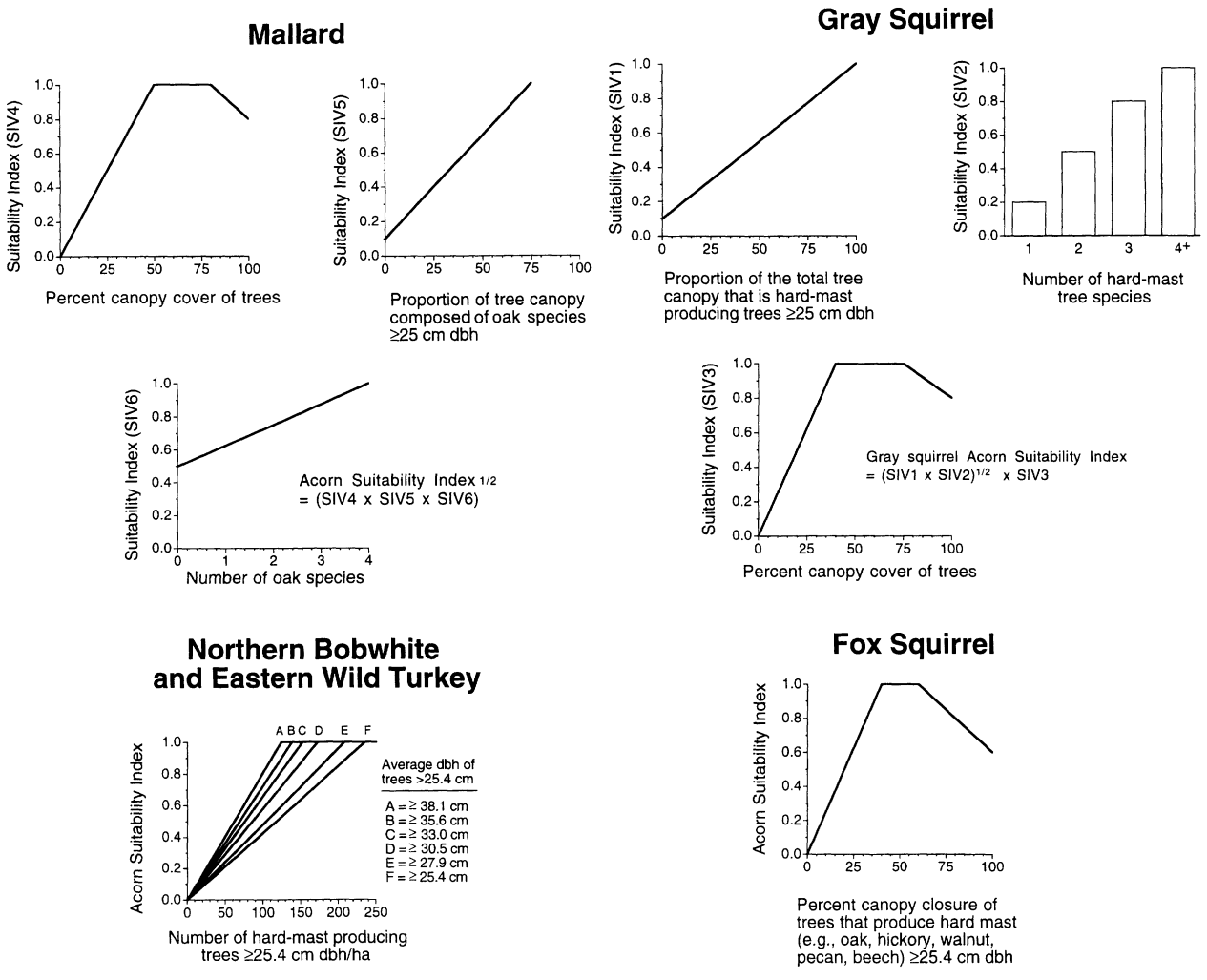


Fig. 1. Habitat variables and suitability index relationships for predicting mast production from the HSI models for mallard, eastern wild turkey, northern bobwhite, gray squirrel, and fox squirrel.

pling acorn production. We nonrandomly selected 3 additional plots on the PRCA to represent areas with open canopies. Oak species in these areas were black oak (*Q. velutina*), white oak (*Q. alba*), scarlet oak (*Q. coccinea*), post oak (*Q. stellata*), chinkapin oak (*Q. muhlenbergii*), northern red oak (*Q. rubra*), Shumard red oak (*Q. shumardii*), and blackjack oak (*Q. marilandica*).

We sampled acorn production systematically, placing 20 traps in each 0.2-ha plot, at a spacing of 7.7 x 8.7 m. Traps were constructed from 6-mil plastic as described in Myers (1978) and Christisen and Kearby (1984). Each trap was 0.73 m in diameter and was suspended above the ground using three 1.52-m pieces of 0.95-cm reinforcement rod. We sampled 8.37 m^2 (0.4%) of each plot with traps.

We collected mast weekly from each plot during 1989–1993, beginning in August when mast began falling and we continued until no further mast was collected from any plot. Mast from each trap was placed in a small paper sack; labeled with the plot number, trap number, and date; and air-dried. Each acorn was identified to species, classified as to maturity, and weighed. After weighing, each nut was cut open to determine soundness. Maturity class and soundness were determined according to Myers (1978) and Christisen and Kearby (1984): classes 1, 2, and 3 (acorn cap completely covers nut; cap surrounding the sides of the nut) were considered immature; classes 4 and 5 (acorn nut nearing full development but green, or fully developed and darkened) were considered mature. We defined acorn crop failure in a given year as production of <6 kg/ha of sound, mature acorns, approximately 10% of the amount Goodrum et al. (1971) estimated as required to support 5 game species for 180 days.

We collected vegetation data for each mast variable in the 5 HSI models (Fig. 1). On each plot, trees ≥15 cm diameter at breast height (dbh) were measured and identified to species. We measured the crown area of mast-producing trees ≥25.4 cm dbh (the diameter of the crown at 0° [north], 60°, and 120° [Hays et al. 1981]). We calculated mean crown diameter from the average of the 3 measurements, which we then converted to area. Only the area of the crown above a plot was included. We determined canopy closure of trees ≥15 cm dbh at and between each acorn trap (36 total measurements) using point-intercept and a plastic tube containing crosshairs (Emlen 1967). Acorn predictions in the eastern wild turkey and northern bobwhite models were based on identical input variables and Suitability Index relationships (Fig. 1); thus, only 1 result is reported for these models.

We summarized number and biomass of acorns for each plot. Simple linear regression and correlation analyses were used to assess relationships between model variables and acorn production. In addition, we used tests for heteroscedasticity (Glejser 1969, Davidian and Carroll 1987, Terrell et al. 1996) to determine if there was a wedge-shaped distribution, and visual assessment of plotted data to determine habitat-imposed upper limits on mast production.

Results

Relative proportions of oaks on selected plots were: black oak (37.5%), white oak (29.7%), scarlet oak (24.2%), post oak (7%), chinkapin oak (1.4%), northern red oak (0.15%), Shumard red oak (0.1%), and blackjack oak (0.05%). Average annual acorn production across the 43 plots ranged from 1.1 to 202.8 kg/ha and from 956 to 86,518 acorns/ha between 1989 and 1993 (Table 1). Tree canopy closure ranged from 11.1 to 97.2%, with 34 of the 43 plots >70%. Plots contained 1–4 species of large oak trees (≥25.4 cm dbh) with an average dbh of 34.1 cm, an average density of 71.4 trees/ha, and an average large oak canopy closure of 24.7%.

Acorn suitability index (ASI) values were computed for each of the 5 original HSI models (mallard, eastern wild turkey, northern bobwhite, fox squirrel, and gray squirrel), using the appropriate variables and formulas from the models. ASI values ranged from 0.06 to 1.0. No plots had an ASI of 0.0, and no plots had zero acorn production. Regression of acorn production on the ASI yielded significant predictive relationships for all 5 models (Table 2).

The most important habitat factors associated with acorn production were related to abundance of large oak trees on the plots (Table 3). Acorn production had a positive association with both the relative proportion of the tree canopy that was in large (>25.4 cm dbh) oak trees, the percent canopy closure of large oak trees, and the number of large oak trees/ha. Acorn production was not associated with the average diameter of oak trees ≥25.4 cm, the percent canopy closure of all trees, or the total number of oak species. Piecewise linear regression of the number of oak species on acorn production indicated a positive association as the number of oak species increased from 1 to 3, but no association beyond 3 species.

In addition to assessing acorn production, we analyzed the relationships between the ASI, habitat characteristics, and the number of acorn-crop failures. The number of crop failures was negatively associ-

Table 1. Acorn production (1989–1993) and habitat summary data (1989) for 43 plots in central Missouri (oak data are for trees ≥25.4 cm dbh).

	Number of oak species	DBH of oak trees (cm)	Canopy cover of all trees (%)	Number of oaks/ha	Proportion of canopy in oaks (%)	Canopy cover of oaks (%)	Acorns (kg/ha)	Acorns (no./ha)
Minumum	1	26.9	11.1	15.0	5.2	4.0	1.1	956
Maximum	4	42.2	97.2	164.9	73.0	70.9	202.8	86,518
Mean	3.14	34.1	76.3	71.4	33.4	24.7	52.0	30,453
Standard deviation	0.77	3.6	17.8	39.2	16.8	13.8	37.1	20,003

ated with the ASI values for the fox squirrel (r = -0.344, P = 0.024), gray squirrel (r = -0.299, P = 0.05), and mallard (r = -0.362, P = 0.017) HSI models. Acorn failure rates were also negatively associated with the proportion of oaks (r = -0.332, P = 0.03), oak canopy closure (r = -0.345, P = 0.023), and oak density (r = -0.302, P = 0.049).

HSI model modifications

A secondary purpose of this study was to determine if we could improve the mast-prediction hypotheses of the 5 HSI models. We searched for patterns through statistical analyses and visual assessments of the plotted data, considering both acorn production and the number of mast failures. Forests with high-potential mast production and low numbers of mast failures should provide the ideal conditions for sustaining mast-consuming wildlife.

We believe a top-down approach (Van Horne and Wiens 1991) is best for developing a simple, logical habitat model. The top-down approach begins with general statements about the system and proceeds by adding details, as needed. A bottom-up approach takes a series of existing models and combines them into a larger, general model; this is not a useful method for modifying the mast-prediction hypotheses of the 5 HSI models. The acorn variables from these models are highly interrelated and are essentially different ways of measuring the same basic attribute—the abundance of large oak trees. A top-down approach should determine the few key variables that best explain the system and result in a single model that can be applied for any wildlife species that consumes acorns.

The 5 HSI models can be split into 2 distinct methods used to predict acorn production: the turkey and northern bobwhite models evaluate the density of oak trees >25.4 cm dbh; the mallard, fox squirrel, and gray squirrel models evaluate the canopy closure of oak trees >25.4 cm dbh. We considered these 2 methods separately for potential model revisions.

Oak tree density model

Maximum acorn production occurred in stands with fewer large oak trees/ha than specified in the original turkey and bobwhite models. In plots with an average oak tree dbh ≥37 cm (considering only oaks >25.4 cm dbh), maximum acorn production occurred with as few as 50 such trees/ha. In stands with an average oak tree dbh of <30.5 cm, maximum acorn production occurred with ≥200 such trees/ha. We used this information to develop a revised relationship between the number and size of oak trees and predicted acorn production (RSIV1; Fig. 2).

The number of oak tree species was not included as a variable in the original turkey, bobwhite, or fox squirrel HSI models but was included in the mallard and gray

Table 2. Regression of acorn production on Acorn Suitability Index (ASI) for 5 species Habitat Suitability Index (HSI) models.

Species model	Regression equation (±95% confidence interval)	R^2	P-value
Mallard	ACPERHA[a] = 15,114 (±24,554) + 72,963 (±38,371) (ASI)	0.265	0.001
	WTPERHA[b] = –11.05 (±49.1) + 101.0 (±76.7) (ASI)	0.147	0.011
Turkey/bobwhite	ACPERHA = 15,991 (±11,822) + 32,007 (±22,916) (ASI)	0.163	0.007
	WTPERHA = 30.95 (±22.7) + 46.68 (±44.1) (ASI)	0.10	0.038
Gray squirrel	ACPERHA = –3,326 (±20,997) + 66,099 (±39,644) (ASI)	0.217	0.002
	WTPERHA = 7.98 (±41.6) + 86.20 (±78.5) (ASI)	0.107	0.032
Fox squirrel	ACPERHA = 7,147 (±12,360) + 39,897 (±19,184) (ASI)	0.301	<0.001
	WTPERHA = 15.69 (±24.3) + 62.23 (±37.8) (ASI)	0.213	0.002

[a] ACPERHA = numbers of acorns/ha.
[b] WTPERHA = kg of acorns/ha.

Table 3. Correlation coefficients for acorn production and habitat factors (oak data are for trees ≥25.4 cm dbh).

	Proportion of canopy in oaks (%)	Canopy cover of oaks (%)	Number of oaks/ha	DBH of trees (cm)	Canopy cover of all trees (%)	Number of oak species (1–3 species only)
Acorns (kg/ha)	$r = 0.312$	$r = 0.399$	$r = 0.385$	$r = 0.199$	$r = 0.204$	$r = 0.07$
	$P = 0.04$	$P = 0.008$	$P = 0.011$	$P = 0.2$	$P = 0.19$	$P = 0.031$
Acorns (no./ha)	$r = 0.424$	$r = 0.458$	$r = 0.289$	$r = 0.127$	$r = 0.117$	$r = 0.465$
	$P = 0.005$	$P = 0.002$	$P = 0.06$	$P = 0.417$	$P = 0.45$	$P = 0.013$

squirrel models. Our data indicated that oak species diversity was positively associated with mast production as the number of oak species increased from 1 to 3. From this information, we developed a revised SI relationship for oak tree diversity (RSIV2; Fig. 3).

We explored various mathematical combinations of the revised variables for oak tree density and oak species diversity. Combining the SI values with a geometric mean provided the best model:

$$\text{Revised oak tree density ASI} = (\text{RSIV1} \times \text{RSIV2})^{\frac{1}{2}}$$

Regression of acorn production on the revised oak tree density ASI (Fig. 4) yielded the following results (±95% confidence intervals):

$$\text{ACPERHA} = 326\ (\pm 16{,}665) + 42{,}471\ (\pm 22{,}255)\ (\text{ASI})$$

$$(R^2 = 0.266,\ P < 0.001)$$

$$\text{WTPERHA} = -1.74\ (\pm 31.3) + 75.8\ (\pm 41.8)\ (\text{ASI})$$

$$(R^2 = 0.246,\ P = 0.001)$$

The plotted data had wedge-shaped distributions, indicating that the revised model was predicting habitat-imposed upper limits on acorn production. Analysis of the absolute values of the residuals of a least absolute deviations regression of these data detected heteroscedasticity in the distributions (ACPERHA, $P = 0.002$; WTPERHA, $P = 0.026$). The revised oak tree density ASI was not significantly associated with the number of acorn crop failures ($r = 0.236$, $P = 0.128$).

Oak tree canopy closure model

Analysis of the models using canopy closure indicated that large (>25.4 cm dbh) oak canopy closure had the strongest correlation with acorn production. Large oak canopy closure is the only input variable used to predict acorn production in the fox squirrel HSI model, and the ASI from this model had the strongest correlation with acorn production of all 5 models. We developed a revised model that included the original fox squirrel variable (Fig. 1) and the revised variable for oak tree species diversity (Fig. 3). The arithmetic mean of these SI values provided the best model:

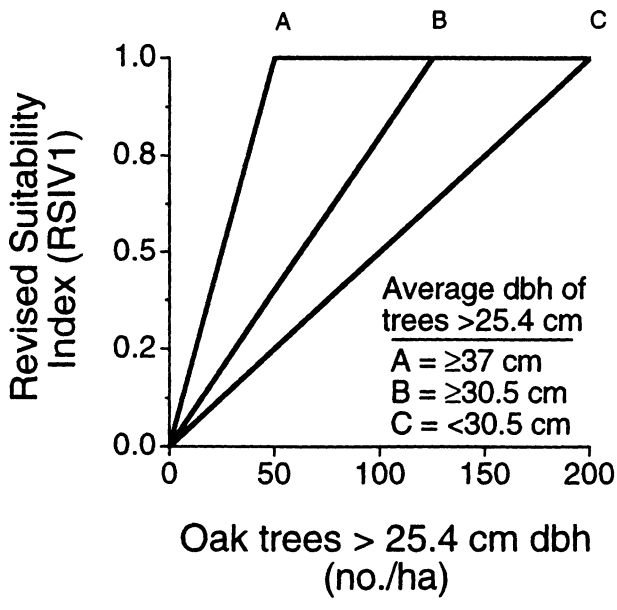


Fig. 2. Revised suitability index relationship for the number of oak trees ≥25.4 cm dbh.

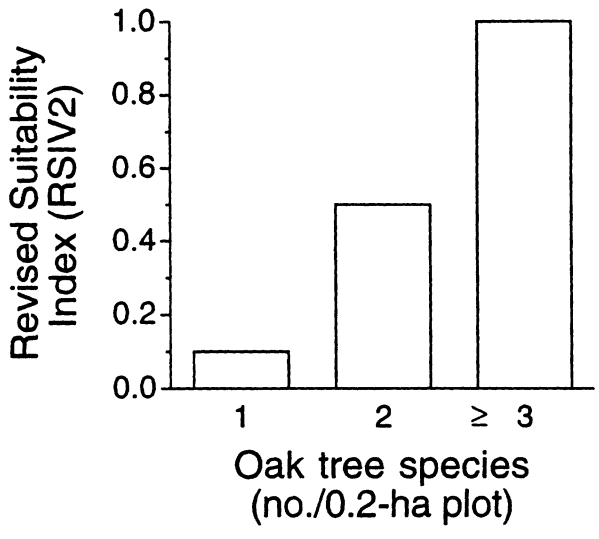


Fig. 3. Revised suitability index relationship for the number of oak tree species.

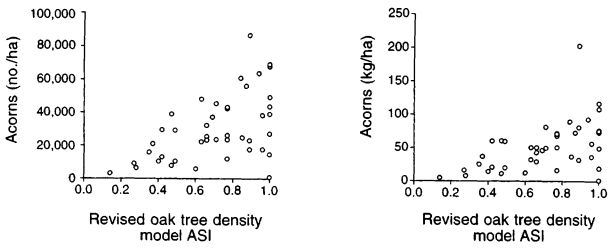


Fig. 4. Plots of acorn production versus the revised oak tree density model Acorn Suitablility Index (ASI).

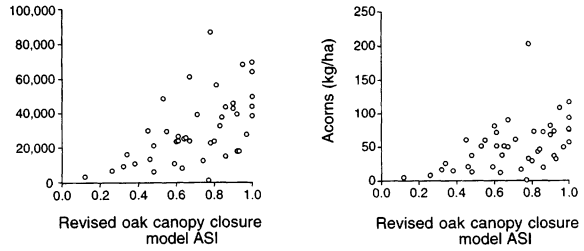


Fig. 5. Plots of acorn production versus the revised oak canopy closure model Acorn Suitability Index (ASI).

Revised oak canopy closure ASI

$$= \frac{(\text{fox squirrel ASI} + \text{RSIV2})}{2}$$

Regression of acorn production on the revised canopy closure ASI yielded the following results (95% confidence interval):

$$\text{ACPERHA} = -4{,}665\ (\pm 16{,}801) + 49{,}886\ (\pm 22{,}728)\ (\text{ASI})$$

$$(R^2 = 0.324,\ P < 0.001)$$

$$\text{WTPERHA} = -2.56\ (\pm 33.3) + 77.55\ (\pm 45.0)\ (\text{ASI})$$

$$(R^2 = 0.227,\ P = 0.001)$$

Visual assessment of the plotted data (Fig. 5) for the revised canopy closure model indicated the model may have been displaying habitat-imposed upper limits to mast production. Tests for heteroscedasticity approached significance with ACPERHA (P = 0.066) but were not significant for WTPERHA (P = 0.192). The revised canopy closure ASI was negatively associated with the number of acorn failures (r = -0.318, P = 0.038).

Discussion

The test of the mast-prediction hypotheses of the 5 HSI models indicated a positive association between acorn production and the model estimate in all cases. The 5 HSI models, however, present 4 slightly different methods to estimate acorn production. A single method with as few variables as possible would be more useful to resource managers. We recommend that managers use the revised oak canopy closure model because it has strong predictive power for acorn production, is negatively associated with number of acorn failures, and has only 2 variables.

None of the original or revised acorn habitat models accounted for >32% of the variance associated with acorn production. An important aspect of testing habitat models, however, is to look beyond linear assessments of central tendency and consider whether the model is a reasonable predictor of habitat-imposed upper limits (Schroeder 1994, Terrell et al. 1996). An early explanation of the use of a habitat-based approach for environmental assessment indicated that such an approach did not include other variables that might act as limiting factors (U.S. Fish and Wildl. Serv. 1980). Terrell et al. (1996) indicated that traditional regression analyses might not identify habitat variables that were limiting factors. The concept of habitat-imposed upper limits implies that regardless of other conditions, acorn production will be limited when habitat conditions are poor. When habitat conditions are excellent, however, acorn production may or may not be high, depending on the influence of the other nonhabitat factors. Plots of data exhibiting a habitat-imposed limit would be expected to have a distribution below the line describing the limit (Fig. 6). The revised oak tree density and oak canopy closure models (Figs. 4 and 5) exhibit this pattern. Where the models predict a low ASI there are no sample plots with high levels of acorn production. The sample plots that have a high ASI and low

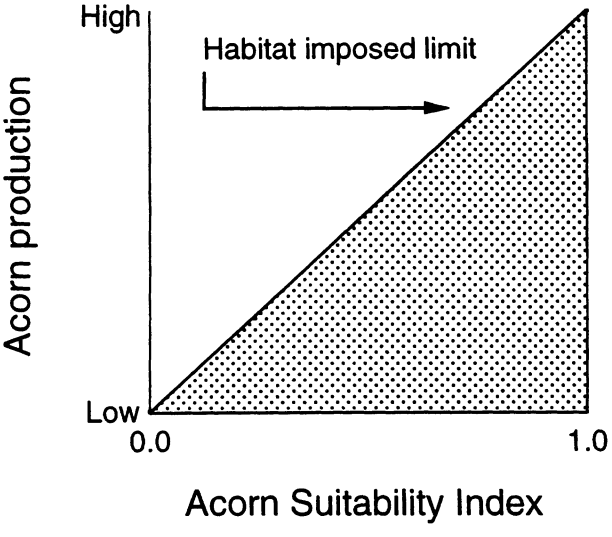


Fig. 6. Conceptual relationship illustrating an upper limit to acorn production imposed by habitat constraints. The shaded area represents values for acorn production that do not invalidate the upper-limit hypothesis.

acorn production do not invalidate the limit hypothesis. The low production on these plots could be a function of nonhabitat factors.

Oak mast production is vary greatly among trees, species, locations, and years (Olson and Boyce 1971). Nonhabitat factors affecting acorn production include inherent genetic characteristics and weather (Christisen and Kearby 1984). The revised oak canopy closure model accounts for 32% of the variance associated with predicting acorn production. A recent study in east-central Missouri found that weather accounted for 55% and 89% of the variance in acorn production in black oak and red oak, respectively, over an 8-year period (Sork et al. 1993), indicating that weather is a dominant factor affecting acorn production. Beck (1989) suggested that because factors such as weather are beyond managers' control, they should strive to provide forests with the highest potential for mast production. Therefore, to maximize the probability of high acorn yields in oak forests, managers should attempt to provide the habitat conditions that promote high mast production. The revised oak canopy closure ASI model should provide reasonable estimates of the habitat conditions required to meet this goal.

Recommendations for future habitat model tests

The test of the mast-production hypotheses of the 5 HSI models supports the concept of upper limits imposed by habitat conditions. Simple linear assessments of data do not necessarily reveal this relationship. Future tests of habitat models should consider the upper-limit concept and the effects of nonhabitat variables.

HSI models were originally intended for use as management tools, applicable to broad geographic areas and in situations where users are limited by time constraints. The general approach to development of these models was consistent with the top-down approach described by Van Horne and Wiens (1991), i.e., beginning with general statements about a system and adding more detail, as needed. We recommend that model tests not lead to the creation of overly complex models with large numbers of variables, but focus, instead, on a top-down approach, using only the key variables needed to explain a system.

A drawback of the top-down approach is that such models frequently fail when applied to conditions other than those used in their development (Van Horne and Wiens 1991), but this is not always the case (Brennan 1991). Our revised acorn model would benefit from tests in other geographic regions of the country, and we recommend broad geographic testing of all general habitat models.

Acknowledgments. We thank D. W. Murphy, D. A. Granfors, J. D. Burk, and D. A. Hasenbeck for coordinating the fieldwork for this study. They were assisted in the field by M. K. Kenney, D. T. Thompson, R. K. Fry, M. T. Pollock, S. J. Schultz, G. E. Sullivan, T. E. Petit, A. W. Gibbs, S. E. Telford, M. W. Wilcoxen, D. V. Hicks, G. W. Smith, M. Szczypinski, T. A. Doumitt, T. E. Duck, III, M. A. Ternent, J. E. Dawson, P. A. Van Winkle, S. M. Couch, and L. M. Johnson. This study was also supported, in part, by the Federal Aid to Wildlife Restoration Act, under Pittman-Robertson Project W-13-R-48. B. S. Cade, A. H. Farmer, S. L. Haire, M. K. Laubhan, J. E. Roelle, D. F. Stauffer, and 1 anonymous reviewer provided comments on the manuscript.

Literature cited

Allen, A. W. 1982. Habitat suitability index models: fox squirrel. U.S. Fish and Wildl. Serv. FWS/OBS-82/10.18. 11pp.

Allen, A. W. 1987*a*. Habitat suitability index models: mallard (winter habitat, Lower Mississippi Valley). U.S. Fish and Wildl. Serv. Biol. Rep. 82(10.132) 37pp.

Allen, A. W. 1987*b*. Habitat suitability index models: gray squirrel, revised. U.S. Fish and Wildl. Serv. Biol. Rep. 82(10.135) 16pp. [First printed as FWS/OBS-82/10.19, Jul 1982.]

Beck, D. E. 1977. Twelve-year acorn yields in southern Appalachian oaks. U.S. For. Serv. Res. Note SE-244. 8pp.

Beck, D. E. 1989. Managing mast production/capability. Pages 24-27 *in* C. E. McGee, ed. Proceedings of the workshop: Southern Appalachian mast management. Univ. Tennessee, Knoxville.

Brennan, L. A. 1991. Regional tests of a mountain quail habitat model. Northwest. Nat. 72:100-108.

Christisen, D. M., and W. H. Kearby. 1984. Mast measurement and production in Missouri (with special reference to acorns). Missouri Dep. Conserv. Terrestrial Ser. No. 13. 34pp.

Cypert, E. 1951. Suggestions for the management of oak forests for mast production. Proc. Southeast. Assoc. Game and Fish Comm. 5:1-7.

Davidian, M., and R. J. Carroll. 1987. Variance function estimation. J. Am. Stat. Assoc. 82:1079-1091.

Downs, A. A., and W. E. McQuilkin. 1944. Seed production of southern Appalachian oaks. J. For. 42:913-920.

Emlen, J. T. 1967. A rapid method of measuring arboreal canopy cover. Ecology 48:158-159.

Glejser, H. 1969. A new test for heteroskedasticity. J. Am. Stat. Assoc. 64:316-323.

Goodrum, P. D., V. H. Reid, and C. E. Boyd. 1971. Acorn yields, characteristics, and management criteria of oaks for wildlife. J. Wildl. Manage. 35:520-532.

Harlow, R. F., and R. L. Eikum. 1963. The effect of stand density on the acorn production of turkey oaks. Proc. Southeast. Assoc. Game and Fish Comm. 17:126-133.

Hays, R. L., C. Summers, and W. Seitz. 1981. Estimating wildlife habitat variables. U.S. Fish and Wild. Serv. FWS/OBS-81/47. 111pp.

MARTIN, A. C., H. S. ZIM, AND A. L. NELSON. 1961. American wildlife and plants: a guide to wildlife food habits. Dover Publ., New York, N.Y. 500pp.

MCGEE, L. E. 1989. A workshop summation. Pages 83-85 *in* C. E. McGee, ed. Proceedings of the workshop: Southern Appalachian mast management. U.S. For. Serv. Cherokee Natl. For. and Univ. Tennessee, Knoxville.

MILLER, M. R. 1981. Ecological land classification. Terrestrial subsystem. A basic inventory system for planning and management on the Mark Twain National Forest. U.S. For. Serv. Eastern Reg., Rolla, Mo. 56pp.

MINCKLER, L. S., AND R. E. MCDERMOTT. 1960. Pin oak acorn production and regeneration as affected by stand density, structure and flooding. Univ. Missouri, Coll. Agric., Agric. Exp. Stn. Res. Bull. 750. 24pp.

MYERS, S. A. 1978. Insect impact on acorn production in Missouri upland forests. Ph.D. Diss. Univ. Missouri, Columbia. 246pp.

OLSON, D. F., JR., AND S. G. BOYCE. 1971. Factors affecting acorn production and germination and early growth of seedlings and seedling sprouts. Pages 44-48 *in* Oak symposium proceedings, U.S. For. Serv. Northeast For. Exp. Stn., Upper Darby, Pa. 161pp.

SCHAMBERGER, M., A. H. FARMER, AND J. W. TERRELL. 1982. Habitat suitability index models: introduction. U.S. Fish and Wildl. Serv. FWS/OBS-82/10. 2pp.

SCHROEDER, R. L. 1985*a*. Habitat suitability index models: Eastern wild turkey. U.S. Fish and Wildl. Serv. Biol. Rep. 82(10.106). 33pp.

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

SCHROEDER, R. L. 1994. Introduction to habitat suitability models. Chap. 5 *in* R. L. Stiehl, ed. Habitat evaluation procedures workbook. Natl. Ecol. Res. Cent., Natl. Biol. Serv., Fort Collins, Colo.

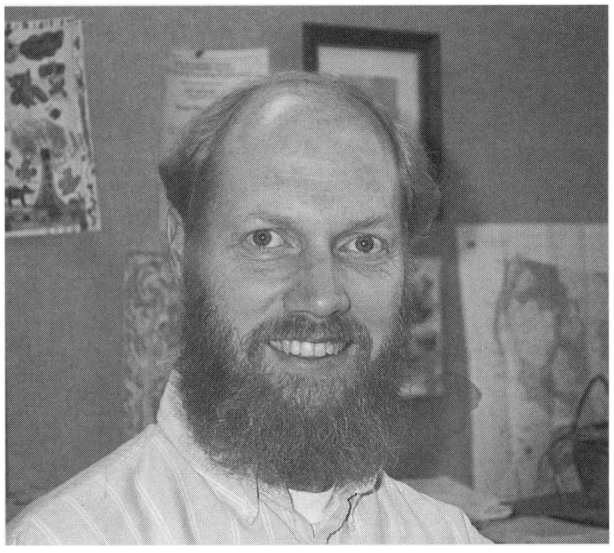
SHAW, S. P. 1971. Wildlife and oak management. Pages 84-89 *in* Oak symposium proceedings, U.S. For. Serv. Northeast For. Exp. Stn., Upper Darby, Pa. 161pp.

SORK, V. L., J. BRAMBLE, AND O. SEXTON. 1993. Ecology of mast-fruiting in three species of North American deciduous oaks. Ecology 74:528-541.

TERRELL, J. W., B. S. CADE, J. CARPENTER, AND J. M. THOMPSON. 1996. Modeling stream fish habitat limitations from wedge-shaped patterns of variation in standing stock. Trans. Am. Fish. Soc. 125:104-117.

U.S. FISH AND WILDLIFE SERVICE. 1980. Standards for the development of habitat suitability index models. Ecol. Serv. Manual 103.

VAN HORNE, B., AND J. A. WIENS. 1991. Forest bird habitat suitability models and the development of general habitat models. U.S. Fish and Wildl. Serv. Fish and Wildl. Res. 8. 31pp.



Richard (Rick) L. Schroeder (photo) is a wildlife biologist with the Biological Resources Division of the U.S. Geological Survey in Fort Collins, Colorado. He received his B.S. in wildlife biology from Colorado State University. Rick's interests include applied research in the area of habitat evaluation, and he has developed several wildlife community habitat models. ***Larry D. Vangilder*** is a wildlife research biologist for the Missouri Department of Conservation. Larry received his B.S. and M.S. in fisheries and wildlife biology from the University of Missouri-Columbia and his Ph.D. in zoology from The Ohio State University. Larry's current research interests include the population ecology of wild turkeys and other vertebrates and the effects of timber management on forest ecosystems. Larry also serves as Missouri's species specialist for wild turkeys.

Associate Editor: Brennan