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Alterations in condition of cottontail rabbits (*Sylvilagus floridanus*) on rangelands following brush management

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Abstract

Although the use of herbicides and prescribed fire have been shown to increase density of cottontail rabbit (*Sylvilagus floridanus*) populations, the impact of such brush management practices on their condition has not been explored. We used discriminant analysis to investigate responses of overall physical condition of cottontail rabbits (n = 422 adults) to brush management and succession on replicated disturbed and undisturbed upland hardwood forest-tallgrass prairie over a 6-year period. Five different disturbed habitat types were experimentally created using herbicides (tebuthiuron or triclopyr), fire, or a combination of both. Parameters that were important discriminators of rabbit physical condition among habitat types and post-disturbance successional changes included indices of kidney fat and parasitism, and relative masses of spleen, liver, and dried stomach digesta. Brush management practices using herbicides influenced overall condition of rabbits, but the type of habitat disturbance was not important. Effects on overall body condition of cottontail rabbits from burning disturbed habitats were not apparent until later seral stages when production of herbaceous dicots declined and vegetative composition more closely resembled that of undisturbed areas.

Key Words: cottontail rabbit, *Sylvilagus floridanus*, body condition, brush management, herbicides, prescribed burning.

Our recent work in an upland hardwood forest-tallgrass prairie in central Oklahoma suggests that habitat disturbance provides important resources for permitting cottontail rabbit populations to increase (Lochmiller et al. 1991). Disturbance resulting from brush management practices effectively alters both cover and nutrient attributes of these rangelands. Recent analyses of forage quality (Bogle et al. 1989) and availability (Engle et al. 1991a, 1991b, Stritzke et al. 1991a, 1991b) on brush-treated rangeland suggest that nutrient alterations are proximate resource factors that stimulate increases in population density following habitat disturbance (Lochmiller et al. 1991).

We hypothesized that improvements in the nutritional quality of forage resources on recently disturbed habitats facilitate an increase in overall physical condition of cottontail rabbits, which ultimately results in increased density. Condition parameters have been widely used to assess responsiveness of lagomorphs to changes in diet quality. Length-weight ratios (Bailey 1968), fat reserves (Henke and Demarais 1990, Lord 1963, Warren and Kirkpatrick 1978), body mass (Bailey 1969, Snyder et al. 1976), and organ-glandular masses (McCreedy and Weeks 1992) have been used to assess changes in habitat quality, dietary intake, or forage quality. Because no single condition index appears universally robust for differentiating among nutritional subpopulations, the use of multivariate approaches that regress several nutritional indices at once has been recommended to improve classification accuracy of subpopulations (Hawley 1987, Hellgren et al. 1989, Jenks 1991, Lochmiller et al. 1985). Discriminant analysis of condition indices has been applied successfully in differentiating among diet groups, metabolic states, and habitat types in a variety of animal species (Hawley 1987, Hellgren et al. 1989, Jenks 1991). Our objective was to use a similar multivariate approach to evaluate the impact of brush management on overall physical condition of cottontail rabbits on replicated disturbed and undisturbed temperate upland hardwood forest-tallgrass prairie. We were particularly interested in physical condition of rabbits in response to post-disturbance secondary succession.

Methods

Study Area

We examined differences in physical condition of cottontail rabbits from replicated habitat types on an area located approxi-

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mately 11 km southwest of Stillwater, Okla. (36°2' to 36°4' N, 97°9' to 97°11' W). Our study area encompassed upland hardwood forest dominated by blackjack oak (*Quercus marilandica* Muenchh.) and post oak (*Q. stellata* Wang.) intermixed with tallgrass prairie invaded by eastern redcedar (*Juniperus virginiana* L.). This area is representative of the cross timbers vegetation type (Ewing et al. 1984), which accounts for nearly 5-million ha of land in Oklahoma, Kansas, and Texas (Soil Conservation Service 1981). Our study area consisted of twenty-four, 32.4-ha (0.42 × 0.83-km) experimental units representing 5 distinct habitat types in various stages of secondary succession, and undisturbed control habitats. Experimental units were arranged in a randomized complete block design with 4 replications of each habitat type. The 5 disturbed habitat types were experimentally created using herbicides, prescribed fire, or a combination to initiate secondary succession. Experimental alterations included: 1) tebuthiuron only or 2) triclopyr only applied aerially at 2.2 kg ha^{-1} in 1983; and combinations of 3) tebuthiuron or 4) triclopyr applied as above followed by late-spring burns in 1985, 1986, 1987 and 1990; and 5) late-spring burns (same burning schedule as above) only with no herbicide application (burned-controls). Undisturbed habitats received no herbicide or prescribed burning and represented virgin upland hardwood forest-tallgrass prairie. All experimental units were grazed by yearling cattle from early spring to fall with the goal of 50% utilization of annual forage production (Stritzke et al. 1991a).

Tebuthiuron caused an intense disturbance and resulted in near total removal of the woody overstory canopy, an effect which persisted throughout the study (Stritzke et al. 1991a, 1991b). Triclopyr was not as efficient as tebuthiuron in controlling resprouting after removal of the oak overstory. Thus, triclopyr habitats contained a mixture of woody species that were released after removal of the dominate oaks in the overstory. The oak overstory of triclopyr habitats was replaced by American elm (*Ulmus americana* L.) and eastern redcedar; the woody understory was dominated by buck brush (*Symphoricarpus orbiculatus* Moench.) (Stritzke et al. 1991a, 1991b). During the first several years after disturbance by herbicide, the understory of habitats was dominated by pioneer forbs and grasses, especially horseweed (*Conyza canadensis* L.) and pokeweed (*Phytolacca americana* L.). Several years after disturbance the understory was dominated by a mixture of annual forbs and grasses, especially rosette panicgrass (*Panicum oligosanthes* Schultes), with increasing amounts of warm-season perennial grasses toward the end of the study (Engle et al. 1991a, 1991b). Burning had little effect on the woody plant communities, except to reduce eastern redcedar invasion on tebuthiuron-altered habitats starting in the 1988 burn year (Engle et al. 1991a, 1991b, Stritzke et al. 1991a, 1991b). However, burning tended to increase forbs in the herbaceous understory (Engle et al. 1991a, 1991b). In general, annual productivity of grasses and forbs increased greatly by disturbance compared to undisturbed areas and was greater in early seral (1987–1988) than late seral (1990–1992) communities (Fig. 1). Disturbance intensities of each habitat type could be ranked as: tebuthiuron plus burned > tebuthiuron > triclopyr plus burned > triclopyr > burned-control > undisturbed.

Data Collection

A total of 422 adult cottontail rabbits (224 female, 198 male) was harvested from experimental habitat types in January and July from 1987 through 1992. Rabbits were not collected in 1989, January 1990, or July 1992 which resulted in 8 sampling periods overall; burned-control habitats were only sampled in January and July 1990-1992. Adults were individuals of >800 g body mass or lighter individuals in reproductive condition. An attempt was made during each sampling period to harvest 5 rabbits from each of 2 replicate habitat types, except summer 1990 when 4 replicates of each habitat type were sampled. All rabbits were harvested shortly after sunset with the aid of a spotlight. To minimize collecting rabbits whose home range encompassed 2 or

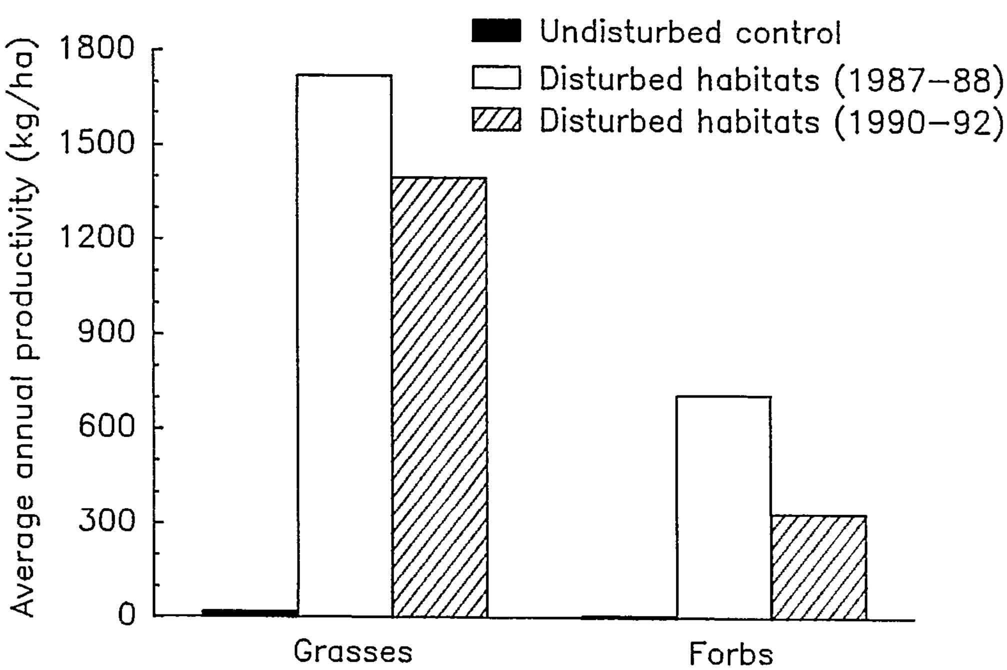

Fig. 1. Average grass and forb production on undisturbed and disturbed (burned and unburned herbicide-altered) upland hardwood forest-tallgrass prairie, by early (1987-1988) and late (1990-1992) seral stages.

more different experimental habitat types, all individuals were harvested at a distance >75 m interior to boundary fences. A previous mark-recapture study indicated that cottontail rabbit movement between habitat types was negligible (Lochmiller et al. 1991).

Gender, body mass, total length (from tip of snout to last caudal vertebrae), and hind-foot length were recorded. Carcasses were necropsied, and masses of spleen, liver, thymus, paired kidneys, paired adrenals, and kidney fat were determined. Intensity of parasitism was indexed by enumerating stomach worms (*Obeliscoides cuniculi*). Rabbits also were classified as nonreproductive, pregnant, lactating, nonscrotal, or scrotal (no difference among treatments; data not shown, but see Peitz 1993). Stomach digesta was removed, and both a wet and dry (lyophilization to a constant mass) mass determined.

Data Analysis

To standardize allometric parameters, relative mass of stomach digesta and organ-glandular tissue was calculated as a percent of whole body mass prior to analysis. Kidney fat was expressed as a percent of total paired kidney mass to derive a kidney fat index of nutritional condition (Riney 1951). Bailey's (1968) index of physical condition was calculated for each individual (reproductive tissues were not subtracted from body mass of pregnant females). Indices of parasitism and kidney fat, lengths, body mass, and relative masses of kidney, spleen, and thymus were rank transformed to normalize their distribution prior to statistical analysis (Conover and Iman 1981).

Influence of habitat type and vegetative succession on individual condition parameters was assessed using a two-way analysis of variance for unbalanced data (PROC GLM; SAS Institute, Inc. 1988) with habitat type and succession as main factors. Successional stages were defined as early seral (years 1987-1988) and late seral (years 1990-1992). A least significant difference test was performed when means for habitat type or successional stage were found to be significantly different ($P<0.05$). Single degree of freedom specific contrasts were used to identify by season, differences in condition parameters between 2 specific treatment categories (unburned herbicide-altered vs. burned herbicide-altered; burned vs. unburned; undisturbed vs disturbed; tebuthiuron-altered vs. triclopyr-altered).

Stepwise discriminant analysis (PROC STEPDISC, SAS Institute Inc. 1988) was used to select reduced sets of discriminator parameters from our overall data set that provided the best overall separation of individual populations among habitat types based on nutritional condition indices. Discriminant analysis (PROC DISCRIM, SAS Institute Inc. 1988) with reduced sets of discriminator parameters (determined by stepwise discriminant analysis) and a jackknife procedure were used to investigate overall condition of rabbits from different habitats and successional stages by season as described by Rice et al. (1983). Two-group comparisons were made for these analyses, with habitats compared as follows: unburned herbicide-altered vs. burned herbicide-altered, burned vs. unburned, undisturbed controls vs. disturbed, tebuthiuron-altered vs. triclopyr-altered, undisturbed controls vs burned-controls. Differences in overall classification accuracies between early and late seral stages for two-group comparisons were analyzed by season using a Z-test of probabilities. Overall comparisons of the effects of habitat type and succession on cottontail rabbit condition were investigated by season using a five-group comparison consisting of undisturbed habitats, early and late seral stages of herbicide-altered habitats, and early and late seral stages of burned herbicide-altered habitats. Canonical discriminant analysis on five-group comparisons was used to further determine relationships among the influences of habitat type and succession on overall condition of rabbits.

Table 1. Physical condition parameters (mean with SE in parentheses) in summer of adult cottontail rabbits (*Sylvilagus floridanus*) as influenced by habitat disturbance and successional stage. Differences among habitat types (T) and successional stages (S) were tested by analysis of variance.

	Habitat disturbance						Successional stage (S)		ANOVA (P <)		
Condition parameter	Tebuthiuron	Tebuthiuron w/fire	Triclopyr	Triclopyr w/fire	Undisturbed	Control w/fire	1987-88	1990-92	T	S	T*S
Body mass (Kg)	1.00(0.03)^{ac}	1.09(0.03)^{b}	0.97(0.04)^{ac}	0.93(0.04)^{a}	1.04(0.03)^{bc}	0.91(0.06)^{ac}	0.98(0.02)	1.01(0.02)	0.01	N	N[d]
Length (mm)											
hind foot	85.0(0.83)	86.4(0.70)	84.9(0.83)	83.5(1.01)	85.6(0.90)	80.7(1.65)	86.9(0.67)^{a}	83.4(0.47)^{b}	N	0.01	N
total body	389.6(5.57)^{ab}	402.8(3.83)^{b}	388.0(5.02)^{a}	380.4(6.52)^{a}	389.7(4.46)^{a}	374.9(9.83)^{a}	384.7(3.76)^{a}	391.4(2.90)^{b}	0.03	0.02	N
Kidney fat index[e](%)	8.24(0.71)	8.46(0.83)	7.75(0.89)	9.76(1.04)	5.91(0.49)	5.84(0.61)	8.66(0.64)	7.36(0.39)	N	N	N
Condition index[f]	12.05(0.39)	12.73(0.32)	11.79(0.35)	11.63(0.49)	12.90(0.39)	11.52(0.86)	12.13(0.27)	12.19(0.23)	N	N	N
Parasitism index	37.8(4.74)	52.3(9.79)	54.5(7.05)	42.3(5.63)	50.0(6.3)	46.9(15.0)	59.2(5.61)^{a}	40.3(3.62)^{b}	N	0.01	N
Relative mass (%)											
Adrenal[g]	14.3(0.60)	14.1(0.50)	15.3(0.60)	14.9(0.60)	15.4(0.40)	14.1(0.60)	14.4(0.40)	15.0(0.30)	N	N	N
Liver[h]	2.21(0.04)	2.18(0.04)	2.27(0.04)	2.28(0.06)	2.19(0.04)	2.32(0.06)	2.24(0.03)	2.23(0.02)	N	N	N
Kidney[h]	0.56(0.01)	0.55(0.01)	0.58(0.01)	0.60(0.02)	0.57(0.01)	0.63(0.03)	0.56(0.01)	0.58(0.01)	N	N	N
Spleen[g]	52.7(4.60)^{a}	61.0(6.10)^{ab}	58.9(5.00)^{ab}	79.3(8.80)^{b}	54.7(5.70)^{a}	108.5(17.00)^{b}	62.0(4.90)	67.5(4.00)	0.03	N	N
Thymus[g]	35.5(3.80)^{a}	26.4(2.20)^{a}	36.0(3.60)^{ac}	46.4(4.10)^{bc}	29.6(3.50)^{a}	35.6(4.90)^{a}	37.1(2.50)^{a}	33.1(1.90)^{b}	0.01	0.03	N
Stomach digesta[h]											
wet	3.07(0.15)	3.14(0.14)	3.42(0.13)	3.29(0.17)	3.14(0.18)	3.01(0.23)	3.74(0.09)^{a}	2.87(0.08)^{b}	N	0.01	0.01
dry	0.49(0.03)	0.49(0.02)	0.55(0.03)	0.49(0.03)	0.46(0.03)	0.50(0.04)	0.51(0.02)	0.49(0.01)	N	N	0.02

[a-c] Means within habitat disturbance or successional stage with the same superscript were not statistically different ($P>0.05$).
[d] Not significant.
[e] Kidney fat index = (kidney fat mass / kidney mass)× 100.
[f] Condition index = (body mass - 251.09) / body length^3.
[g] [parameter mass (mg) / body mass (g)] × 100
[h] [parameter mass (g) / body mass (g)] × 100.

Table 2. Physical condition parameters (mean with SE in parentheses) in winter of adult cottontail rabbits *(Sylvilagus floridanus)* as influenced by habitat disturbance and successional stage. Differences among habitat types (T) and successional stages (S) were tested by ANOVA.

Condition parameter	Habitat disturbance: Tebuthiuron	Tebuthiuron w/fire	Triclopyr	Triclopyr w/fire	Undisturbed	Control w/fire	Successional stage (S): 1987-88	1990-92	ANOVA (P <): T	S	T*S
Body mass (Kg)	1.01(0.02)	1.05(0.02)	1.03(0.02)	1.05(0.02)	1.05(0.02)	1.06(0.02)	1.03(0.01)	1.05(0.01)	N	N	N[e]
Length (mm)											
hind foot	86.1(0.62)	86.6(0.66)	86.7(0.55)	86.0(0.49)	87.0(0.69)	86.2(0.51)	86.6(0.46)	86.3(0.24)	N	N	N
total body	400.6(3.18)	404.2(2.99)	400.1(2.90)	406.0(2.41)	406.1(2.76)	401.7(4.93)	407.5(1.84)^{a}	399.4(1.59)^{b}	N	0.01	N
Kidney fat index[f] (%)	79.38(9.02)	74.51(7.29)	82.55(10.15)	75.48(7.63)	82.48(9.76)	107.34(12.76)	38.02(2.98)^{a}	119.86(4.16)^{b}	N	0.01	N
Condition index[g]	11.83(0.27)	12.01(0.23)	12.12(0.26)	11.93(0.23)	11.96(0.25)	12.56(0.31)	11.51(0.15)^{a}	12.48(0.14)^{b}	N	0.01	N
Parasitism index	14.5(3.71)	13.3(5.84)	19.3(8.31)	11.3(2.98)	11.1(3.50)	2.4(1.26)	22.7(4.24)^{a}	4.1(0.65)^{b}	N	0.01	N
Relative mass (%)											
Adrenal[h]	15.2(0.70)	14.7(0.60)	16.0(0.60)	14.6(0.70)	14.9(0.50)	15.3(0.90)	15.2(0.50)	15.0(0.30)	N	N	N
Liver[i]	2.78(0.07)^{a}	2.60(0.05)^{c}	2.57(0.06)^{bc}	2.43(0.07)^{bd}	2.51(0.06)^{bc}	2.29(0.08)^{d}	2.48(0.04)^{a}	2.62(0.04)^{b}	0.01	0.01	0.02
Kidney	0.56(0.01)^{a}	0.54(0.01)^{ac}	0.52(0.01)^{bc}	0.54(0.02)^{ab}	0.51(0.01)^{b}	0.52(0.01)^{ab}	0.53(0.01)	0.53(0.01)	0.01	N	0.01
Spleen[h]	51.0(7.20)^{a}	40.9(3.50)^{a}	41.1(3.60)^{a}	39.1(2.80)^{a}	30.8(2.40)^{b}	34.9(3.50)^{ab}	41.6(3.40)	38.7(1.70)	0.02	N	0.02
Thymus[h]	18.2(1.90)^{a}	17.8(1.80)^{a}	14.0(1.40)^{a}	18.2(2.70)^{a}	15.3(1.70)^{a}	13.7(1.80)^{a}	11.7(0.90)^{a}	19.4(1.10)^{b}	0.04	0.01	N
Stomach digesta[i]											
wet	2.27(0.14)	2.42(0.14)	2.44(0.16)	2.24(0.12)	2.60(0.21)	1.97(0.23)	2.87(0.09)^{a}	1.90(0.08)^{b}	N	0.01	0.01
dry	0.40(0.04)^{a}	0.37(0.02)^{ab}	0.40(0.04)^{a}	0.31(0.02)^{b}	0.44(0.03)^{a}	0.35(0.04)^{ab}	0.39(0.02)	0.37(0.02)	0.04	N	0.01

[a-d] Means within habitat disturbance or successional stage with the same superscript were not statistically different (*P*>0.05).
[e] Not significant.
[f] Kidney fat index = (kidney fat mass / kidney mass) × 100.
[g] Condition index = (body mass - 251.09) / body length^3.
[h] [parameter mass (mg) / body mass (g)] × 100.
[i] [parameter mass (g) / body mass (g)] × 100.

Results

No clear trends were evident from univariate comparisons of the 13 condition parameters that we measured in adult cottontail rabbits with respect to influences of habitat type and succession (Tables 1 and 2). During summer, body mass, total body length, and relative masses of spleen and thymus of cottontail rabbits differed (*P*<0.05) among habitat types. During winter, relative masses of liver, kidney, spleen, thymus, and dried stomach digesta differed (*P*<0.05) among habitat types. Relative masses of spleen and thymus were the only 2 condition parameters of rabbits to vary among habitat types in both summer and winter.

Successionally, the parasitism index and relative wet mass of stomach digesta were greater (*P*<0.05) in rabbits harvested from early seral stages than late seral stages during summer and winter (Tables 1 and 2). During summer, relative thymus mass and hind foot length of rabbits were greater, and total body length was less (*P*<0.05) in early than late seral stages. Total body length of rabbits in winter was greater and relative masses of thymus and liver and indices of physical condition and kidney fat were less (*P*<0.05) in early than late seral stages. Interactions between habitat type and succession (*P*<0.05) were observed for relative stomach digesta wet mass of rabbits harvested in both summer and winter, and relative masses of spleen, dried stomach digesta, liver, and kidney in winter. Least significant difference tests of means when main effects were significant revealed no consistent trends in the influence of habitat types on cottontail rabbit condition (Tables 1 and 2).

Single degree of freedom contrasts helped clarify differences (*P*<0.05) in condition parameters among habitat types within each season. During summer, altering habitats with tebuthiuron increased body mass (10%) over those altered with triclopyr; total body length was 3% larger on tebuthiuron- than triclopyr-altered habitats (Table 1). These differences were not reflected in the physical condition index. Relative masses of thymus (33%) and kidney (6%) of rabbits were greater on triclopyr-altered than tebuthiuron-altered habitats in summer. On average, relative spleen mass of rabbits was 50% greater on burned than unburned habitats in summer. Rabbits harvested from disturbed habitats had a kidney fat index that averaged 36% and a relative thymus mass that averaged 22% greater than those harvested from undisturbed habitats during summer.

During winter, relative masses of spleen (34%) and kidneys (5%) of cottontail rabbits were greater (*P*<0.05) on disturbed than undisturbed habitats (Table 2). Relative masses of dried stomach digesta (20%) and liver (7%) were larger in rabbits harvested from unburned than burned habitats during winter. Relative masses of dried stomach digesta (18%) and liver (6%) also were greater in rabbits harvested from unburned herbicide-altered than burned herbicide-altered habitats during winter. Relative liver mass averaged 8% greater for rabbits harvested from tebuthiuron-altered than triclopyr-altered habitats.

Seasonal two-group comparisons of condition indices between habitat categories using discriminant analysis provided overall classification accuracies that were indicative of an influence of habitat disturbance on cottontail rabbit condition (Table 3). Highest overall classification accuracies (78% and 77%) were associated with comparisons of condition between rabbits from undisturbed habitats and those from either disturbed or burned-control habitats. Among two-group comparisons between disturbed habitat types, very similar overall classification accuracies were evident regardless of disturbance type (range = 59–74%). This suggested that the type of disturbance was not as influential on rabbit condition as the fact a habitat was disturbed.

Unlike winter, overall classification accuracies for all two-group comparisons in summer were not significantly (*P*>0.05) different between early and late seral stages (Table 3).

Table 3. Classification accuracies (%) by season, for two-group comparisons of cottontail rabbits *(Sylvilagus floridanus)* from undisturbed and disturbed habitats undergoing secondary succession. Classification accuracy was determined by discriminant analysis of habitat classes based on their influence on condition parameters (selected by stepwise discriminant analysis).

Habitat type comparisons	Early seral stage 1987-1988 Summer	Early seral stage 1987-1988 Winter	Late seral stage 1990-1992 Summer	Late seral stage 1990-1992 Winter
	----------- (%) -----------			
Herbicide-altered	59.0	63.3	64.4	67.7
vs				
Burned herbicide-altered	64.1	57.1	53.5	81.1
Overall	61.5	60.2	58.9	74.4
Burned	64.1	61.9	51.8	79.7
vs				
Unburned	61.7	63.8	60.7	64.4
Overall	62.9	62.9	56.2	72.0
Undisturbed	66.7	81.8	67.9	60.0
vs				
Disturbed	68.8	73.2	70.7	63.7
Overall	67.7	77.5	69.3	61.6
Tebuthiuron-altered	80.5	62.8	85.0	74.4
vs				
Triclopyr-altered	40.0	69.2	34.0	65.9
Overall	60.2	66.0	59.5	70.1
Undisturbed	--	--	64.3	75.0
vs				
Burned-control	--	--	73.9	79.0
Overall			69.1	77.0

Classification accuracies for comparisons between unburned herbicide-altered and burned herbicide-altered habitats increased significantly ($P<0.05$) from early to late seral stages in winter. Classification accuracies for comparisons between undisturbed and disturbed habitats in winter declined significantly ($P<0.05$) from early to late seral stages. Other two-group comparisons showed no significant ($P>0.05$) change in classification accuracy with succession in winter.

The number of times each condition parameter was selected by stepwise discriminant analysis for inclusion into specific two-group comparisons (Table 3) was calculated to determine which parameters were consistent predictors of habitat-induced alteration of rabbit condition (Table 4). Relative spleen mass and kidney fat index were the most important condition parameters for classifying rabbits according to habitat type; parasitism index, relative liver mass, and stomach digesta dry mass also were consistent predictors. Body mass was the least sensitive physical condition indicator for cottontails.

Because specific contrasts indicated that most differences in selected condition parameters were attributable to time post-disturbance, herbicide alteration, or burning of habitats, we used a five-group discriminant analysis to simultaneously compare overall condition of rabbits as influenced by habitat quality. Discrimination of individual cottontail rabbits, based on overall condition, to their original habitat type (undisturbed, herbicide-altered, or burned herbicide-altered) and seral stage, yielded an overall classification accuracy of 55% in summer and 63% in winter (Table 5). Similar to two-group comparisons, overall classification accuracy of rabbits to habitat type and seral stage in five-group comparisons was significantly ($P<0.05$) higher in winter than in summer. Discriminating variables selected by stepwise discriminant analysis for inclusion into our five-group classification model were relative stomach digesta wet and dry masses, body mass, body and hind foot length, and kidney fat and parasitism indexes in summer. In winter, selected parameters were relative masses of wet and dried stomach digesta, thymus, kidneys, liver, kidney fat index, and parasitism index.

Table 4. Number of times each condition parameter was a significant discriminator variable (determined by stepwise discriminant analysis) in our two-group comparisons (Table 3) of overall condition of cottontail rabbits *(Sylvilagus floridanus)* from different habitat types.

Condition parameters	Early seral stage (1987-1988) Summer	Early seral stage (1987-1988) Winter	Late seral stage (1990-1992) Summer	Late seral stage (1990-1992) Winter	Total	Mean
	---------------- (%) ----------------					
Body mass	0	2	0	0	2	0.50
Hind foot length	2	2	1	0	5	1.25
Total body length	0	4	0	1	5	1.25
Kidney fat index	0	2	2	4	8	2.00
Condition index	0	2	3	0	5	1.25
Parasitism index	0	3	2	2	7	1.75
Relative masses						
Adrenal	3	2	1	0	6	1.50
Liver	1	2	0	4	7	1.75
Kidney	0	2	0	2	4	1.00
Spleen	2	4	1	1	8	2.00
Thymus	0	2	0	1	3	0.75
Stomach digesta						
wet	1	2	0	1	4	1.00
dry	0	3	2	2	7	1.75

Canonical discriminant analysis produced centroid means (Fig. 2) clearly indicating that cottontail rabbit condition was influenced by habitat disturbance and seral stage (Table 6 lists weighted coefficients for each condition parameter in the canonical variates). Mahalanobis distances between centroid means of undisturbed habitats and either herbicide-altered (early and late seral stage) or burned herbicide-altered (late seral stage in summer, early and late seral stages in winter) habitats were significantly ($P<0.05$) separated in summer and winter. Mahalanobis distances between the 2 disturbed habitat types in early seral stages separated significantly ($P<0.05$) from those in late seral stages in winter; however, only herbicide-altered habitats in early seral stages separated from the 2 disturbed habitat types in late seral stages in summer. Mahalanobis distances between centroid means of burned and unburned disturbed habitats were only significant ($P<0.05$) in winter of late seral stage.

Canonical variate I in summer represented a gradient of increasing kidney fat index, and to a lesser degree increasing parasitism index, and decreasing relative spleen mass; canonical variate II represented a gradient of increasing physical condition and parasitism index and decreasing relative stomach digesta dry mass. In winter, canonical variate I represented an increasing gradient of kidney fat index, and to a much lesser degree relative stomach digesta dry mass, and decreasing relative kidney mass; canonical variate II represented a gradient of increasing relative masses of liver and spleen, and parasitism index. Seral stage groups separated along canonical variate I in winter and summer. Burned and unburned groups separated along canonical variate II in winter.

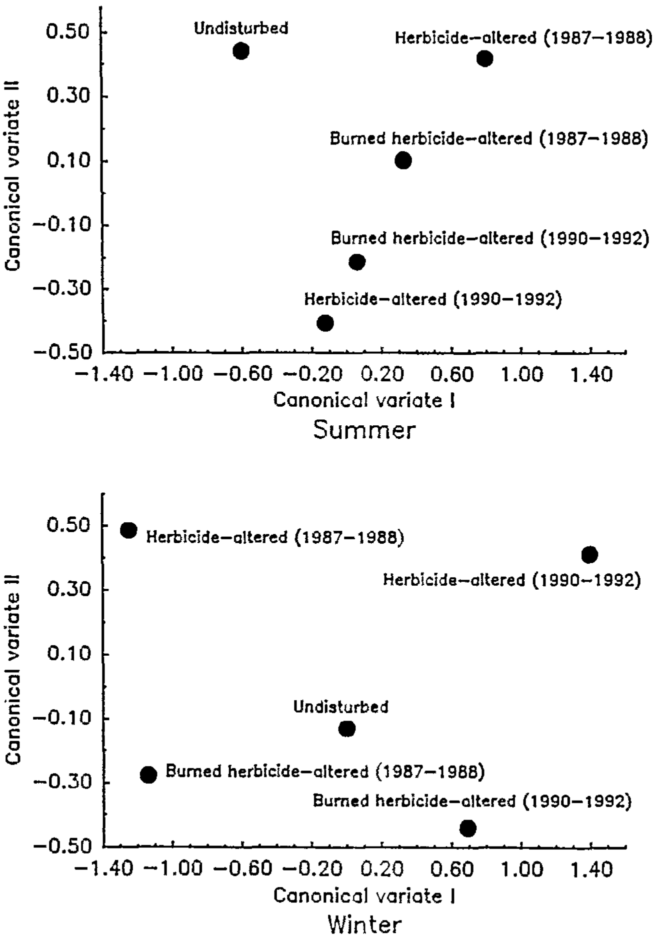

Fig. 2. Graphical representation of separation of canonical variate means for undisturbed and disturbed (burned and unburned herbicide-altered) habitats undergoing secondary succession. Significance of each condition parameter used in a canonical variate is listed elsewhere (see Table 6).

Discussion

Cottontail rabbits are habitat generalists and inhabit a variety of disturbed and transitional habitat types (Chapman et al. 1982). Lochmiller et al. (1991) found variable results in population response to specific habitat disturbances on our study area; however, rabbits showed a positive response to general habitat disturbance and a preference for burned habitats. Inconsistency in how and what individual condition indicators responded to type of habitat disturbance probably reflected the complex nutritional changes that occurred in the environment (not just simply altering energy or protein) and differing sensitivities of these indicators to specific nutrient limitations. This was supported by variations in the number of times each condition indicator was selected by stepwise discriminant analysis as an important parameter for inclusion into specific two-group comparisons. Several condition parameters were repeatedly selected during specific seasonal or seral stage comparisons.

Kidney fat and parasitism indices, and relative masses of spleen, liver, and dried stomach digesta were the most frequently selected predictors of habitat disturbance and seral stage. Our selection of these and other indices of condition for use in assessing how habitat disturbance influences condition in cottontail rabbits was made after review of a variety of literature on lagomorphs and other small mammalian herbivores. We know of no study which has explored the sensitivity of these collective indices in cottontail rabbits to changes in habitat quality.

Table 5. Classification accuracies (%) by season, for five-group comparisons of cottontail rabbits *(Sylvilagus floridanus)* from undisturbed habitats and disturbed (burned and unburned herbicide-altered) habitats undergoing secondary succession. Classification accuracy was determined by discriminant analysis of habitat classes based on their influence on condition parameters (selected by stepwise discriminant analysis for each season).

Habitat type (seral stage)	Summer	Winter
	(%)	
Herbicide-altered (early, 1987-1988)	53.3	54.8
Burned herbicide-altered (early, 1987-1988)	64.7	78.3
Herbicide-altered (late, 1990-1992)	58.5	60.0
Burned herbicide-altered (late, 1990-1992)	59.3	73.7
Undisturbed	39.5	48.7
Overall	55.1	63.1

Kidney fat index is a reflection of stored energy reserves (Flux 1971) and is routinely used to assess physical condition in a variety of animal species. Although captive feeding-trials have indicated that this fat index is sensitive to short-term nutritional stress (Henke and Demarais 1990), its use in field-assessments of lagomorph condition have been limited (Flux 1971). The parasitism index has been shown to vary with changes in habitat quality (Boggs et al. 1990) but does not necessarily increase with decreased habitat quality. Spleen mass varies in response to different environmental stressors, including food shortages (Chapman et al. 1982; Henke and Demarais 1990), crowding (Conaway and Wight 1962), and hemoparasitism (Watkins et al. 1991). Liver mass is influenced positively by the rate of nutrient assimilation (Koong et al. 1985) and presence of secondary plant metabolites (Bergeron and Jodoin 1989). Digesta dry mass reflects dietary bulk intake, which decreases when crude protein in the diet of lagomorphs decreases (Bailey 1969; Bookhout 1965; Sinclair et al. 1982). Lack of a clear trend in univariate statistics and known variations in the response of condition parameters to habitat quality demonstrated a need for a multivariate approach in determining trends in physical condition of cottontail rabbits.

Discriminant analyses provided a multivariate perspective of how habitat disturbance influenced the overall condition of cottontail rabbits. These analyses indicated that disturbance, either from overstory removal with herbicides or burning, altered the overall condition of animals on our study area. Analyses also showed that post-disturbance effects were temporary. The majority of the observed differences and changes in condition are thought to be attributable to disturbance- and successional-induced effects on the nutritional quality of the habitat, as suggested by changes in herbaceous forage production and nutrient composition. One of the most dramatic disturbance-induced changes in the vegetation was herbaceous forb production. The importance of forbs in the diet of cottontail rabbits is due to their digestibility (Bailey 1969; Bogle et al. 1989) and protein content (Bogle et al. 1989).

Table 6. Coefficients for condition parameters used to separate by season five-group comparisons of cottontail rabbits *(Sylvilagus floridanus)* from undisturbed and disturbed (burned and unburned herbicide-altered) habitats undergoing secondary succession in canonical discriminant analysis.

	Summer canonical variate		Winter canonical variate	
Condition parameter[a]	I	II	I	II
Condition index	-0.14	0.79	0.06	0.22
Relative spleen mass (%)	-0.35	-0.07	-0.09	0.52
Relative stomach digesta dry mass (%)	0.26	-0.45	0.33	0.31
Relative liver mass (%)	0.02	-0.38	0.21	0.74
Parasitism index	0.39	0.61	-0.17	0.62
Kidney fat index (%)	1.04	-0.01	1.20	-0.01
Relative kidney mass (%)	0.02	0.06	-0.36	-0.47

[a] See Table 1 for description of condition parameters

Classification accuracy of individual cottontail rabbits into appropriate unburned and burned habitats was high (i.e., undisturbed habitats and burned-controls), suggesting that fire had a major influence on populations. The effects of burning disturbed habitats also were more apparent in later than early seral stages as indicated by improved classification accuracies and significant separation between burned and unburned groups. As described by Engle et al. (1991b), burning was effective at prolonging positive effects of herbicide-induced disturbance with respect to forb production. Five-group comparisons using canonical analysis also indicated that influences of burning on condition were more prevalent in winter than summer (Fig. 2). Increased density of cottontail rabbit populations following prescribed burning has been reported (King et al. 1991) and attributed to improved nutritional conditions (Lochmiller et al. 1991). Prescribed burning has been repeatedly shown to improve nutritional quality (Allen et al. 1976; Hallisey and Wood 1976) and production of herbaceous forages in a variety of habitat types. Similar observations have been reported for our study area (Bogle et al. 1989; Engle et al. 1991b; Soper et al. 1993).

Two-group and five-group comparisons of individual cottontail rabbits from undisturbed and disturbed upland hardwood forest-tallgrass prairie also suggested that habitat disturbance had a significant influence on overall condition of cottontail rabbits. Habitat disturbances on our study area using herbicides to remove woody overstory vegetation significantly improved nutritional quality and production of herbaceous (Bogle et al. 1989; Engle et al. 1991b) and woody forages (Stritzke et al. 1991a; Soper et al. 1993).

Initially, each herbicide removed the oak-dominated overstory (Stritzke et al. 1991a, 1991b), resulting in dramatic increases in the production of herbaceous forbs following release. Fast growing early-seral dominants such as these have been shown to contain greater tissue nitrogen concentrations but are gradually replaced by slower-growing plants as soil nitrogen resources become depleted (McLendon and Redente 1992). Similar successional changes occurred on our study area several years after herbicide disturbance; pioneer forb production declined with succession on both herbicide-altered habitat types (Engle et al. 1991a, 1991b), and eastern red cedar has invaded. This successional change in vegetation was reflected in both two-group and five-group discriminant comparisons. Classification accuracy for comparisons between undisturbed and disturbed habitats declined from early to late seral stages. Five-group canonical analyses revealed significant separation (Mahalanobis distances) between early and late seral stages for both burned and unburned herbicide-disturbed habitats. These separations were most evident in winter.

The degree and similarity in separations of individuals between the various disturbed habitat types using two-group comparisons suggested that overall physical condition of cottontail rabbit was not as dependent on intensity of habitat disturbance as it was to disturbance itself. Classification accuracies were greater for comparisons between undisturbed vs disturbed or undisturbed and burned controls compared to all others (triclopyr vs tebuthiuron, burned herbicide- vs unburned herbicide-altered, burned vs unburned). These results indicate that spatial and temporal changes in habitat quality does influence overall condition of cottontail rabbits. Univariate comparisons were not sufficiently discriminating to detect changes in cottontail condition under these experimental environments. The relationship of habitat-induced alterations in condition to intrinsic population attributes such as recruitment and survival rates were not addressed. However, changes in population density that we observed with habitat disturbance on the study area (Lochmiller et al. 1991) suggest that such a relationship existed. Only adult rabbits were monitored; condition among juveniles may be more disparate among disturbance types.

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