Testing Leopold's Law of Dispersion on Cottontail Rabbits Occupying Shrubland-Grassland Ecotones

Jonathan G. Young
Scott E. Henke
Ralph L. Bingham
Campus Box 218, Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, Texas, USA 78363-8202

ABSTRACT

Leopold's law of dispersion, commonly referred to as the principle of edge, is a long-held tenet of wildlife management. The law suggests that a direct linear relationship exists between the densities of edge-benefitted species and the quantity of edge. We tested three hypotheses derived from edge theory and used cottontail rabbits (Sylvilagus floridanus) as our animal model. Our hypotheses were: (1) an edge-benefitted species will exist in the absence of edge, (2) each species has an edge saturation value (maximum length of edge/area) where additional edge will not increase species density, and (3) there exists a distance from edge, defined as the radius of full use, beyond which a species' use of an area declines. Cottontail rabbits were found in the absence of edge only with shrubland habitat. Cottontails did not exhibit an edge saturation value. The radius of full use for cottontail rabbits was undefined and 3.1 yds in shrubland and grassland, respectively. Data collected in this study did not support current theories concerning the relationship between length of edge and species density.

KEY WORDS: Cottontail rabbit, ecotone edge, Law of Dispersion, *Sylvilagus floridanus*

Leopold's (1933:132) law of dispersion, sometimes referred to as the principle of edge, is often cited in wildlife management texts (Giles, 1978; Robinson and Bolen, 1984; Hunter, 1990), and is used extensively by wildlife managers (Laudenslayer, 1984). However, before a principle is accepted as a law, it must (1) originate as an hypothesis, (2) be upgraded to a theory after considerable evidence is collected in support of the general principle, and finally, (3) be accepted as law after withstanding rigorous testing in which the principle occurs with unvarying uniformity under the same conditions (Bronowski, (1973:240). This has not been the case with the law of dispersion. Although the concept of edge effect has received much attention in the scientific literature (see Reese and Ratti, 1988; Yahner, 1988 for reviews), no researcher, to our knowledge, has specifically collected data in an attempt to refute the law of dispersion. Edge theory has been accepted as fact based upon casual observation (Giles, 1978; Robinson and Bolen, 1984) and upon studies incorporating the edge effect into their design (Hanson and Miller, 1961; Patton, 1975; Galli *et al.* 1976; Gates and Mosher, 1981; Eberhardt, 1990). Edge effect has been defined as the changes in a community due to the creation of abrupt edges in areas of previously undisturbed habitats (Soulé, 1986). Although certain "edge effects" have been documented to increase with increases in the amount of edge such as rates of predation (Wilcove, 1985; Yahner and Scott, 1988), rates of parasitism (Gates and Gysel, 1978, Brittingham and Temple, 1983), and species diversity (Rosenzweig, 1995), such edge effects were not the original intent of Leopold (1933).

The law of dispersion, as originally proposed by Leopold (1933: 132), states that "the potential density of game of low radius requiring two or more types is, within ordinary limits, proportional to the sum of the type of peripheries." Unfortunately, wildlife professionals have derived various interpretations of this statement. Some have stated that as habitat interspersion increases, the density of wildlife species as a unit will increase proportionately (Robinson and Bolen, 1984), while others erroneously expressed that species diversity and abundance will increase proportionately (Yahner, 1988; Barnes *et al.,* 1991). Robbins (1979) stated that the theory only applies to certain edge-obligate species. Guthery and Bingham (1992) argued that the constraints placed on the law by Leopold (1933:132) have been ignored; therefore, past interpretations are erroneous. They offered a revision of the edge principle, but like the original principal, empirical data has been lacking to support their conclusions.

Our objective was to determine if Leopold's law of dispersion is a viable interpretation of a possible relationship between the density of edge-obligate species and edge in a southern Texas shrubland-grassland habitat. Three hypotheses were derived from equations and text in Guthery and Bingham (1992) and were tested separately. Hypothesis one involved the concept that edge-benefitted species will exist in the absence of edge. In other words, density of edge species will be greater than zero in shrubland or grasslands areas that do not contain edge (see Guthery and Bingham, 1992 for the equation and graphical depiction). Hypothesis two stated that each species has an edge saturation value where additional amounts of edge will no longer yield an increase in density (for graphical representation, see Guthery and Bingham, 1992:341). Hypothesis three suggested that the probability of use will remain constant out to a perpendicular distance of r from the edge, to be called the radius of full use, where the probability of use then will decrease monotonically to 0 for distances greater than r from the edge (Fig. 1). Cottontail rabbits were chosen as animal models because they (1) inhabit diverse habitats including open prairies, shrublands, and woodlands (Chapman *et al.,* 1980), (2) are a species of low radius requiring two or more habitat types (Janes, 1959; Robinson and Bolen 1984), (3) have an affinity for high contrast grassland-shrubland edge (Smith 1950), (4) increase in abundance by the creation of edge (Chapman *et al.,* 1980), and (5) have a high relative abundance in southern Texas.

MATERIALS AND METHODS

Definitions

Because of the numerous interpretations of Leopold's (1933:132) concept, it is prudent to define each component to avoid ambiguity. The passage begins ". . . the potential density of . . .", which we interpret to mean the maximum sustained mean density of a species that can indefinitely inhabit an area. Based on Leopold's original description in *Game Management* (1933:132), we interpret ". . . game of low radius requiring two or more types . . ." as any species that can not travel great distances in a short period of time and needs two or more habitat types in close proximity to provide its basic requirements (i.e., food, cover, space, water) for survival. In other words, an edge species spends all or most of its time at or near edges (Johnston, 1947; Forman and Godron, 1986;

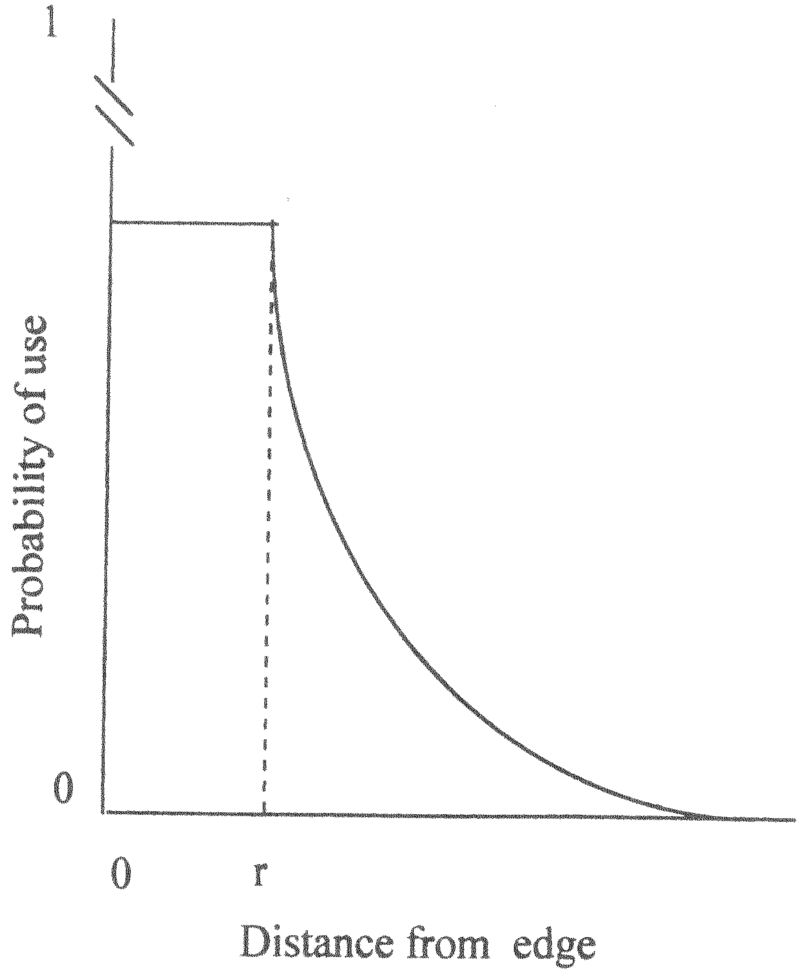

Figure 1. Graphic portrayal of the radius of full use (r).

Yahner, 1988). This includes cottontail rabbits, northern bobwhites (*Colinus virginianus*), and white-tailed deer *(Odocoileus virginianus)*. In contrast, game of high radius would include migratory species such as bison *(Bison bison)*. While species of high radius may require more than one habitat type, the types need not be adjacent. Guthery and Bingham (1992:340) suggested that Leopold (1933:132) added the phrase "... within ordinary limits ..." as an apparent qualifier to explain circumstances where the theory did not apply. Finally, we interpret the phrase "... the sum of the type peripheries" to mean the total perimeter of the interspersed habitat types (sensu Patton, 1975; Thomas *et al.*, 1979). However, edge created by adjoining habitat types should be included only once.

Because many different types of edge exist (Giles, 1978; Thomas *et al.*, 1979), it is prudent to explicitly define it. Edge is a transition zone between two habitat types, which in this study, was between shrubland and grassland habitat types. Only high-contrast edge (i.e., ecotones ≤10 yds wide) was used. An area was considered shrubland if it contained >405 woody stems/acre, average woody stem circumference >1.0 inch, average height of woody species >1.5 yds, and canopy cover >50%. An area was considered grassland if it was composed predominantly of grasses (>75%), contained <10 woody stems/acre that were >1.0 inch in circumference, and had brush canopy cover <10%.

Study Area

The three hypotheses were tested on the 2,100 acre DuPont Chemical, Inc. property (Victoria Co.), the 2,000 acre La Copita Research Area (Jim Wells Co.), the 125 acre Marvin and Marie Bomer Wildlife Management Area (WMA) (Duval Co.), the 210,540 acre Santa Gertrudis Division of the King Ranch (Kleberg Co.), and the 200 acre Trant Ranch (Kleberg Co.) in southern Texas. Southern Texas is characterized as mixed grassland-shrubland habitat, where the chief industries include cattle and oil production, and wildlife enterprises. Predominant grasses on the study sites included King Ranch bluestem *(Bothriochloa ischaemum)*, Kleberg bluestem *(Dicanthlum annulatum)*, johsongrass *(Sorghum halepense)*, kleingrass *(Panicum coloradum)*, and windmillgrasses *(Chloris* sp.), while predominant woody species included honey mesquite *(Prosopis glandulosa)*, live oak *(Quercus virginiana)*, and huisache *(Acacia farnesiana)*. The topography is nearly flat to gently sloping and the soils range from clay to sandy loam (Miller, 1982). Mean annual rainfall ranged from 26 to 38 in., increasing from west to east (Miller, 1982). Mean temperature is 72 F with average lows of 43 F in January and average highs of 93 F in July (National Oceanic and Atmospheric Administration, 1994).

Forty acre sites within each study area were selected based on criteria previously outlined for grassland and shrubland habitat. Density of woody stems was determined using belt transect methodology (Burnham *et al.*, 1980). We walked three 325-yd transects within perspective grassland and shrubland habitat types and measured the height and circumference of each woody stem within 10 yds of the transect line. By doing so, approximately 10% of each perspective study site was assessed to verify that specified site parameters were met. Line intercept method was used to estimate percent canopy cover on each transect line (Canfield, 1941). Transect lines within each area were pooled to estimate density of woody stems, average woody stem height and circumference, and percent canopy cover.

Hypothesis 1: Edge-benefitted Species Will Exist in the Absence of Edge

The densities of cottontail rabbits were determined using line transect methodology with a finite boundary (Burnham *et al.*, 1980:17) from June through October 1995. A finite boundary of 16 yds from the transect line was used because that was the maximum distance that a cottontail rabbit could be detected due to vegetation cover. Eight transects were walked within the grassland and shrubland habitat types >220 yds from any edge to determine rabbits use of non-edge habitat. Cottontail movements were verified using radio telemetry (for details see Hypothesis 3: A radius of full use exists). The largest home range of a cottontail rabbit during this study was estimated to be 8.6 acres (averaging size of home range of cottontails during our study was 5.0 ± 0.4 ac; $\overline{X}$ ± SE). This is

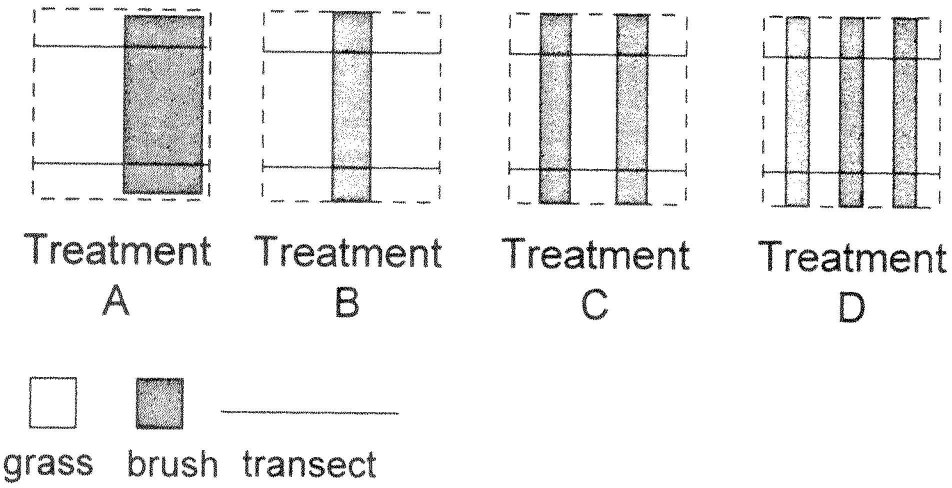

Figure 2. Schematic of 4 different edge lengths in grassland-shrubland ecotones of southern Texas during winter 1995. Each dashed-line square represents a 25-acre area and there were 3 25-acre areas for each edge length class, for a total of 12 25-acre areas. Treatments A, B, C, and D consisted of an average of 345, 688, 1,379, and 2,066 yds of edge length, respectively.

an area equivalent to a square with 204-yd sides. However, cottontail rabbit home ranges typically are elliptical with the long axis of the home range parallel to edge (Althoff, 1983). Therefore it was assumed that cottontails encountered during transects did not have home ranges encompassing edge. Grassland transects were 396, 403, 450, and 533 yds in length and shrubland transects were 261, 321, 495, and 620 yds in length. Each transect was walked ≥5 times during both day and night. Daytime transects were walked during the first and last hour of daylight. Nighttime transects were walked ≥1 hour after sunset and a hand-held 500,000 candle-power spotlight was used to aid detection of animals (Fafarman and Whyte, 1979). The order of the transects was chosen randomly to reduce the bias of reaching the same portion of the transect during the same time interval. Perpendicular distances at which cottontail rabbits were observed from the transect line were determined with a tape measure. Cottontail densities were estimated using the Fourier estimator from program TRANSECT (Burnham *et al.*, 1980). Although >40 objects should be seen on a transect for a precise estimate of density (Burnham *et al.*, 1980:37), our goal was not to provide an estimate but rather to document the presence or absence of animals. The presence or absence of animals was used to determine if animal density was greater than zero in areas with no edge.

Hypothesis 2: Each Species Has an Edge Saturation Value

Twelve 25-acre study areas comprising four edge treatments were chosen (Fig. 2). Treatment A areas had 342, 345, and 347 yds of edge length, treatment B areas had 684, 688, and 692 yds of edge length, treatment C areas had 1,369, 1,377 and 1,390 yds of edge length, and treatment D areas had 2,039, 2,068, and 2,092 yds of edge length. The mean length of edge for each treatment was 345, 688, 1,379, and 2,066 yds, respectively (Fig. 2). Edge length was defined as the cumulative length of edge between shrubland and grassland habitat types contained within a 25-acre area. Edge length in each area was measured using a distance measuring wheel (Rolatape Distance Measuring Wheel, Forestry Suppliers, Inc., Jackson, Miss.).

An index of relative abundance for cottontail rabbits was estimated by scent station methodology from 4 February to 4 March 1996 (Drew *et al.*, 1988). Scent station methodology was selected because it yielded more precise estimates of cottontail relative abundance than nighttime headlight counts (Drew *et al.*, 1988). Each 25-acre area contained two transect lines 110 yds apart, which were approximately perpendicular to the shrubland-grassland edge. The 25-acre areas were >220 yds from each other. Transect lines were used as scent station lines. Each line consisted of 11 scent stations located at 32-yd intervals, which yielded 66 scent stations per treatment. Scent stations were located in grassland and shrubland habitats within each treatment in equal proportion. Each scent station consisted of a 1-yd circular plot of sifted soil that was cleared of debris and vegetation. Scent capsules consisted of perforated, plastic discs (HistoPrep tissue capsules, Fisher Scientific, Pittsburgh, Penn.) that contained cotton saturated with a synthetic lure (W-U lure, Fagre *et al.*, 1983). Scent capsules were placed in the center of each circular plot and were elevated about 2 inches above ground with a 3-inch nail. Scent capsules were placed on the stations in the afternoon and stations were checked the following day. Each station was recorded as either "visited" or "not visited"; species visitation was determined by track identification. An index of relative abundance was calculated for cottontail rabbits by dividing the number of visited stations by the number of operable scent stations per area each night (Linhart and Knowlton, 1975). Scent capsules were removed from the plots after each use to avoid habituation to the lure by cottontail rabbits. Scent station lines were repeated three times; ≥7 days expired between scent station line repetitions.

The index of abundance for cottontail rabbits was determined for each 25-acre area using pooled (2) transect lines. A completely randomized treatment structure with repeated measures was used to test the effect of edge length and time on the ranks of the indices of abundance for cottontail rabbits (Conover and Iman, 1981). Mean separations for the means of the ranks were made using Tukey's HSD procedure when a significant ($P < 0.05$) F-test was noted. Indices of abundance for cottontails, which were pooled across areas and time, were regressed against the 12 (i.e., three areas within four treatments) edge lengths to develop predictive equations using linear (Cody and Smith, 1991:104) and quadratic equations.

Hypothesis 3: A Radius of Full Use Exists

The radius of full use by cottontails was determined using radio telemetry. A total of 15 cottontails from DuPont Chemical, Inc. property, LaCopita Research Area, and Bomer WMA was captured with 6.6 × 8.5 × 28.3 in. wooden box traps. Each rabbit was fitted with a 150.000 Mh, 2 to 4-in. variable-circumference radio collar (L. L. Electronics, Mahomet, Ill.). Hourly locations of each cottontail rabbit was determined to simulate a 72-hour period. Radio-tracking of cottontails was conducted on La Copita, Dupont Chemicals, Inc. property, and Bomer WMA from 20 June–9 July 1995, 29 July–23 August 1995, and 8 September–2 October 1995, respectively. Each cottontail was tracked for nine 8-hour periods, from 0001 h to 0800 h, 0801 h to 1600 h, and 1601 to 2400 h, which consisted of three repetitions for each 8-hour period. Cottontails were tracked for one 8-hour period each day. Depending on capture success and animal location, multiple cottontails often were tracked concurrently. Radio locations were visually verified and marked with a numbered stake. Perpendicular distance from edge to each radio location was measured using a measuring wheel (Rolatape Distance Measuring Wheel, Forestry Suppliers, Inc., Jackson, Miss.). Distance (yds) and compass direction from a known point to each stake was recorded and plotted on an aerial map. Home range was determined by the 95% minimum convex polygon method (Dixon and Chapman, 1980) using program TELEM88 (Coleman and Jones, 1988).

Frequency distributions of cottontail rabbit hourly locations were plotted against the distance from edge (yds) for grassland and shrubland habitats. A spline model consisting of a horizontal line segment joined to an exponential curve with unknown knot was used to determine the estimated radius of full use (*r*; horizontal coordinate of knot). Because the partial derivative of the model with respect to the parameter used to specify the radius of full use is not continuous, the corresponding asymptotic standard error and confidence interval limits may not be correct. In general, this discontinuity can disturb convergence of the iterative process employed by SAS PROC NLIN (SAS Inst., Inc., 1991), which uses maximum likelihood estimation for nonlinear models, giving different results depending on different specified starting values for the parameters of the model. The model employed was:

$$Y = b_0/(b_1 - 1) \text{ for } 0 \leq X < r \text{ or } b_0/(b_1 - EXP(b_2 \times (X - r))) \text{ for } X \geq r$$

with parameters b_0, b_1, b_2, and r, where r is the radius of full use. For a wide range of reasonable starting values, convergence was obtained to essentially identical parameter estimates, with identical asymptotic standard errors, correlations, and 95% confidence interval limits for the radius of full use.

RESULTS

Hypothesis 1: Edge-benefitted Species Will Exist in the Absence of Edge

Six cottontails were observed on 11.6 miles of transects in shrubland habitat >220 yds from edge. This resulted in a density estimate of 0.13 cottontails/ac in shrubland. However, cottontails were not observed on any grassland transects (44.7 miles) >220 yds from edge. Overall cottontail density in the absence of edge (shrubland and grassland transects pooled) was estimated to be 0.027 cottontails/ac.

Hypothesis 2: Each Species Has an Edge Saturation Value

Ranks of relative abundance indices for cottontail rabbits differed (F = 11.94; 3,8 df; P = 0.0025) between edge lengths (Fig. 3). Mean index of abundance for cottontails was greatest for 345 yds of edge length ($\bar{x}$=0.20), followed by 2,066 ($\bar{x}$=0.17), 1,379 ($\bar{x}$=0.10), and 688 m of edge length ($\bar{x}$=0.03). No time effect (F=1.59; 2, 16 df; P=0.2350) or treatment by time interaction (F=1.69; 6,16 df; P=0.188) were observed.

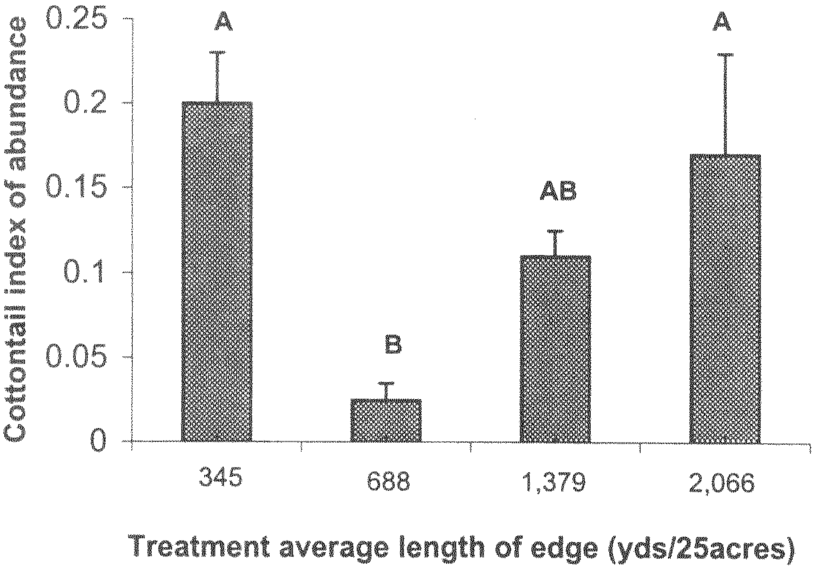

Figure 3. Cottontail rabbit mean index of abundance (proportion of scent stations visited by rabbits, $n = 66$) in relation to edge lengths in southern Texas grassland-shrubland ecotones during winter 1995–1996. Bar heights are actual mean index values and the terminal horizontal bars represent standard errors for cottontail index of abundance. Statistical analysis was conducted on ranked means of abundance. Rank means with the same letter did not differ ($P>0.05$) by Tukey's HSD test.

Linear models, as suggested by Leopold (1933), using the indices of abundance and arcsine transformation of indices of abundance for cottontails for each of the 12 different edge lengths, were not significant [($F=3.28$; 1,34 df; $P=0.08$; $R^2=0.09$) and ($F=1.55$; 1,34 df; $P=0.22$; $R^2=0.04$)], respectively. A predictive equation using untransformed indices of abundance for cottontails yielded the linear model: cottontail index of abundance = 0.00004(edge length/area) + 0.06.

A posteriori quadratic model using the indices of abundance for cottontail rabbits was significant ($F=9.79$; 2,33 df; $P=0.0005$; $R^2=0.37$). A predictive quadratic equation for cottontail index of abundance is 0.00000018 (edge length/area)^2 − 0.00037 (edge length/area) + 0.22.

Hypothesis 3: A Radius of Full Use Exists

Cottontail rabbits averaged over all 3 areas were found to travel a mean distance of 27.5 ± 30.1 yds ($\bar{x} \pm SE$; $n = 15$) into shrubland and 36.8 ± 27.5 yds into grassland from edge. The greatest distances traveled into shrubland and grassland by cottontails were 155 yds and 143 yds, respectively. The estimated radius of full use for grasslands was 3.1 yds with asymptotic 95% confidence interval limits of 2.8 yds and 3.5 yds ($R^2=0.956$). Radius of full use by cottontails in shrubland was undefined by the spline model and therefore was graphically estimated as 0 yds. However, 60%, 77%, and 85%

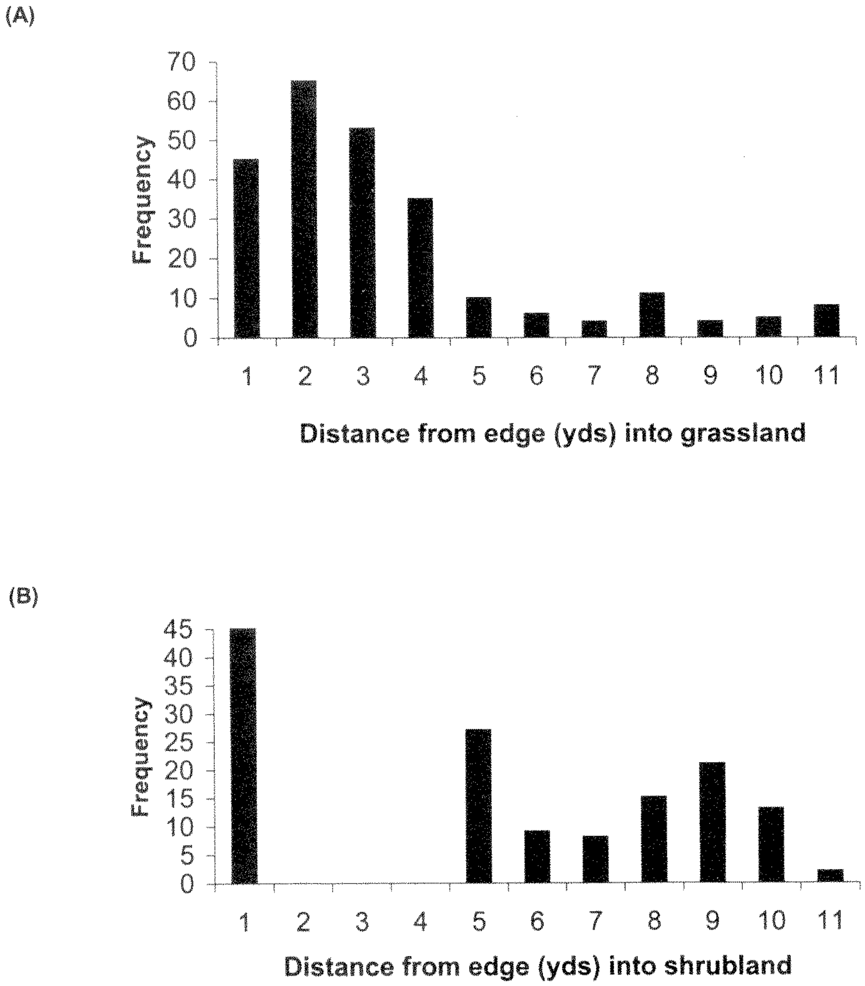

Figure 4. Frequencies of cottontail rabbit locations in (A) grassland and (B) shrubland habitat of southern Texas during summer 1995, with respect to distance (yds) from edge.

of cottontail activity was concentrated within 16, 32, and 49 yds of edge, respectively (Fig. 4). The greatest home range of a cottontail rabbit was 8.6 ac.

DISCUSSION

Empirical data were collected to examine the law of dispersion as originally outlined by Leopold (1933:132) and modified by Guthery and Bingham (1992). Our data did not fully support either theoretical model. Leopold (1933:132) suggested that edge-related species would not exist in the absence of edge, whereas Guthery and Bingham (1992) argued that edge-related species could exist in areas without edge. However, our data were ambivalent concerning this point. Cottontail rabbits were not observed in grasslands away from edge, which supports Leopold's (1933:132) theory; however, they were observed in shrublands, albeit few individuals, which favors the idea of a positive intercept as proposed by Guthery and Bingham (1992). Although our definition of shrubland included a canopy cover >50%, which constituted extremely dense brush, patches of open areas within the shrubland did exist. Such open areas intermixed within dense vegetation effectively could have been perceived by cottontails as edge. Fagan *et al.* (1999) realized that other species may visually perceive edges differently than humans. Morrison *et al.* (1992:32) recognized that humans only can hypothesize how animals perceive their environment and deemed this concept niche gestalt. Therefore, it only may be possible to determine if cottontail rabbits exist in the absence of edge within a shrubland if the shrubland has 100% canopy cover. Unfortunately, large tracts of land with 100% canopy cover are extremely rare because of current land-use practices, so such an hypothesis may not be testable using this habitat type.

Neither Leopold's (1933:132) nor Guthery and Bingham's (1992) model provided an adequate interpretation of cottontail rabbit data concerning hypothesis two. Leopold (1933:132) suggested a direct relationship between the densities of edge-related species and quantity of edge, whereas Guthery and Bingham (1992) argued that the Leopold model would hold true up to an edge saturation value where the potential density of a species would not be greater for additional edge, but beyond which, an inverse relationship would exist between densities of edge and edge-related species. However, abundance of cottontail rabbits exhibited a positive quadratic function with regards to increasing lengths of edge, which may have resulted from predator avoidance. Chapman and Tretheway (1972) noted that cottontail predation risk was directly related to distance traveled away from edge.

Redundant edge, as defined by Guthery and Bingham (1992), did not occur for cottontail rabbits on our study areas. Optimum edge density for cottontail rabbits was 1,462 yds/acre, according to the equation outlined by Guthery and Bingham (1992:343). Therefore, habitat that contains optimum edge density for cottontails would be quite patchy, such as a shrubland intermixed with open areas that do not exceed 6.2 yds from refuge cover (i.e., $2r$, where r = radius of full use). Cottontail rabbits may prefer patchy habitat as a means to avoid predators and temperature extremes. Cottontails are known to use brushpiles, hedgerows, and dense brush for escape (Chapman *et al.*, In Pennsylvania, cottontail rabbits select resting and bedding sites to avoid cold temperatures (<32 F; Althoff *et al.*, 1997); however, cottontails in southern Texas used resting sites <0.5 yd from shrub stems probably to escape hot (>95 F) rather than cold temperatures. Similar behavior of heat avoidance has been noted in other species in southern Texas (Kopp *et al.*, 1998).

We recognize that our interpretations of our results are dependent on our definitions of habitat parameters. For example, different results might have been obtained in our study had shrubland, grassland, and ecotone been defined differently. Yahner (1988) also recognized this problem and suggested that a standardized protocol for measuring and comparing edge effects in different landscapes be developed. Definitions of edge species, edge dimensions, edge age and structure, plant community types, and methods of quantifying edge effects need to be considered *a priori* (Yahner, 1988). Yahner (1988) also believed that additional studies of edge effect are needed because greater quantities of edge will be created in future landscapes due to current land-use practices.

Creation of edge was emphasized to past wildlife professionals as being beneficial to wildlife because it was widely believed that wildlife was a product of habitat interspersion

(Yoakum and Dasmann, 1971; Harris, 1988). However, recent research suggests that creation of additional edge does not always positively affect wildlife (Harris, 1988). Edges can modify distribution and dispersal of wildlife species and attract nest parasites and predators (Harris, 1988; Temple and Cary, 1988), reduce the size of large tracts of habitat necessary to interior species and cause isolation of patches and corridors (Yahner, 1988), and cause deleterious effects of herbivores on sensitive plant species (Alverson *et al.*, 1988).

Although the original premise by Leopold (1933:132) does not appear to hold true for all edge-related species and not all species are benefitted by the creation of edge, the relationship between ecotones and wildlife is intriguing and worthy of investigation. According to the definition of a scientific law (Bronowski, 1973:240), Leopold's (1933:132) law of dispersion should not be considered 'a law' because the principle does not occur with unvarying uniformity. However, it does provide a framework of ecological theory from which the more complex interactions of community ecology can be addressed.

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Box T-0050
Tarleton State University
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