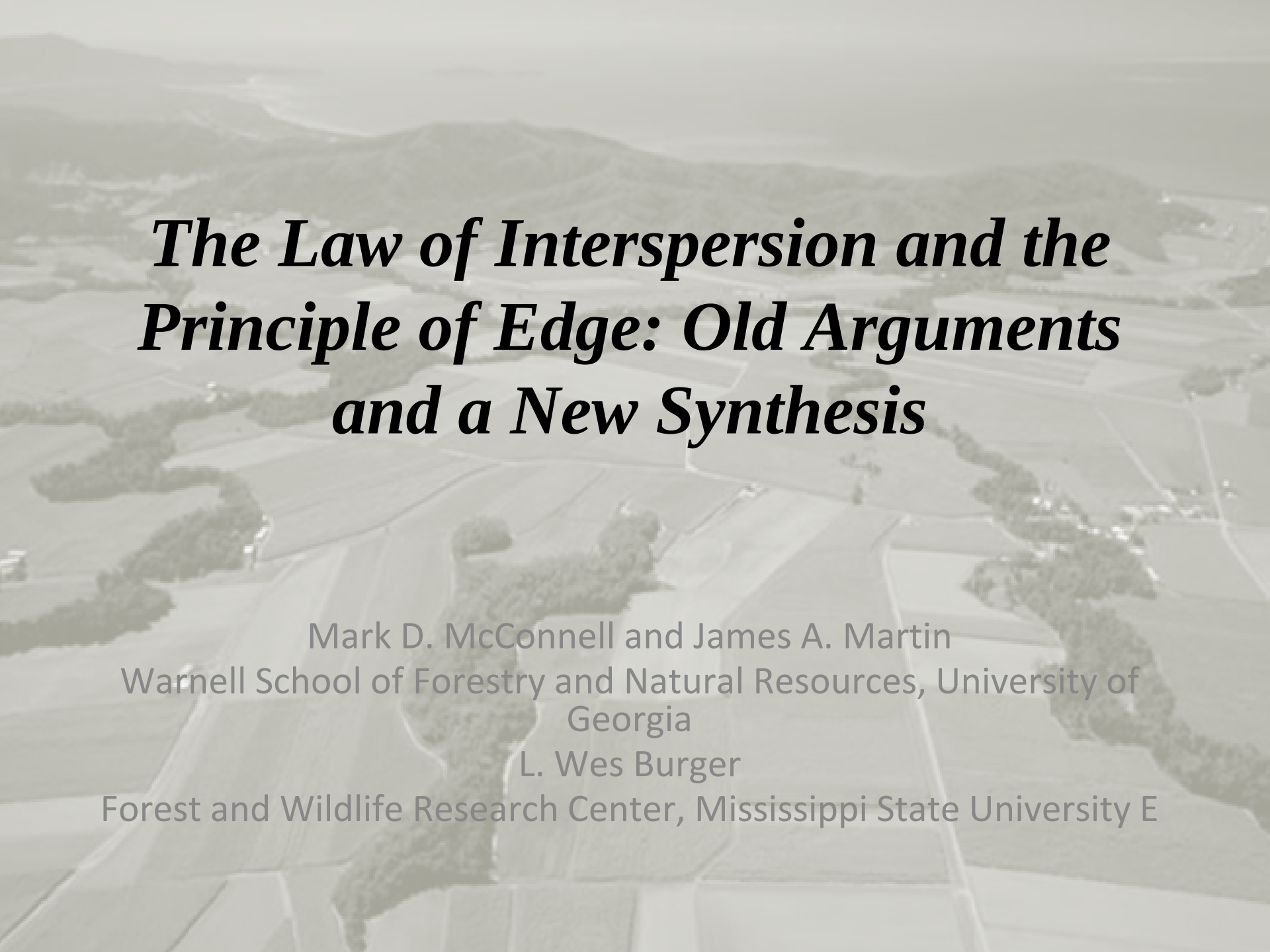


The background of the slide is a grayscale aerial photograph of a rural landscape. It shows a patchwork of agricultural fields, some with distinct patterns, and a winding river or stream that flows through the scene. In the distance, there are rolling hills or mountains under a hazy sky. The overall tone is serene and naturalistic.

The Law of Interspersion and the Principle of Edge: Old Arguments and a New Synthesis

Mark D. McConnell and James A. Martin

Warnell School of Forestry and Natural Resources, University of
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Outline

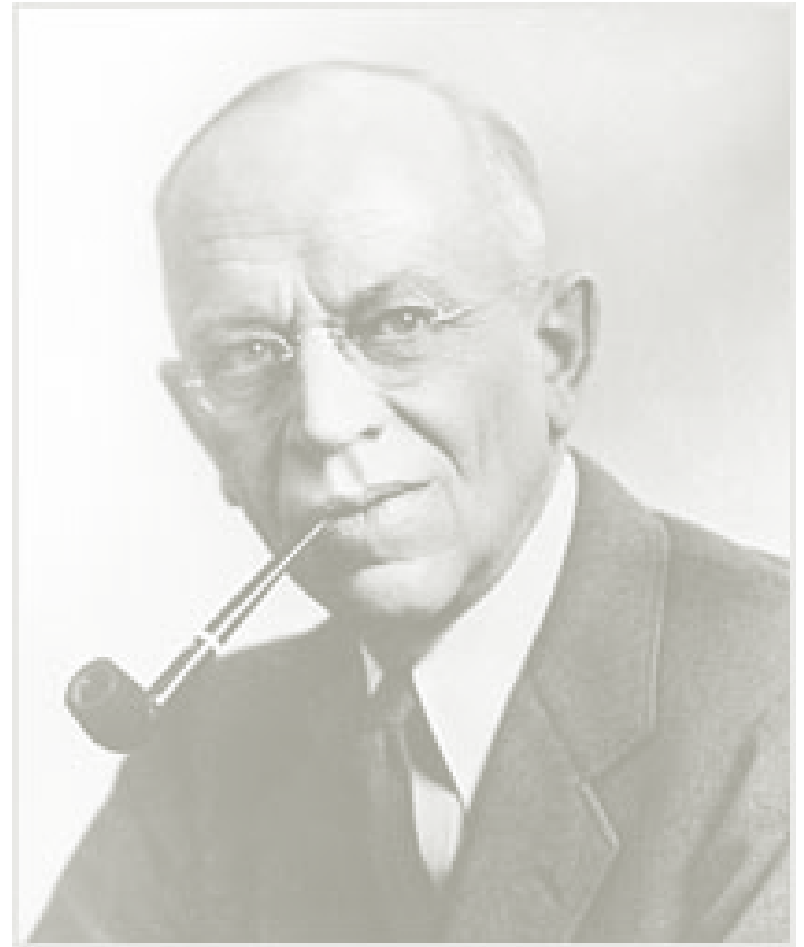
- Historical Roadmap
- What Leopold Actually Wrote
- What (*we think*) Leopold Meant
- What Leopold Did Not Write
- Guthery's Characterization
- Misconceptions
- Results from Mississippi and Texas
- Musings
- Future Directions

Law of Interspersion Roadmap

- 1933 – *Law of Interspersion* described by Aldo Leopold in Game Management
- 1961 – *Edge Types and Abundance of Bobwhites in Southern Illinois* – Hanson and Miller
- 1972 – *The Interspersion Index as a Technique for Evaluation of Bobwhite Quail Habitat* – Baxter and Wolf
- 1992 – *On Leopold's Principle of Edge* – Guthery and Bingham
- 1997 – *A Philosophy of Habitat Management for Northern Bobwhite* – Guthery

What did Leopold Actually Write?

- “The maximum population of any given piece of land depends, therefore, not only on its environmental types or composition but also on the **interspersions of these types** in relation to the cruising



What did Leopold Actually Write?

- “Composition and **interspersions** are thus the two principle determinants of potential abundance of game range.”



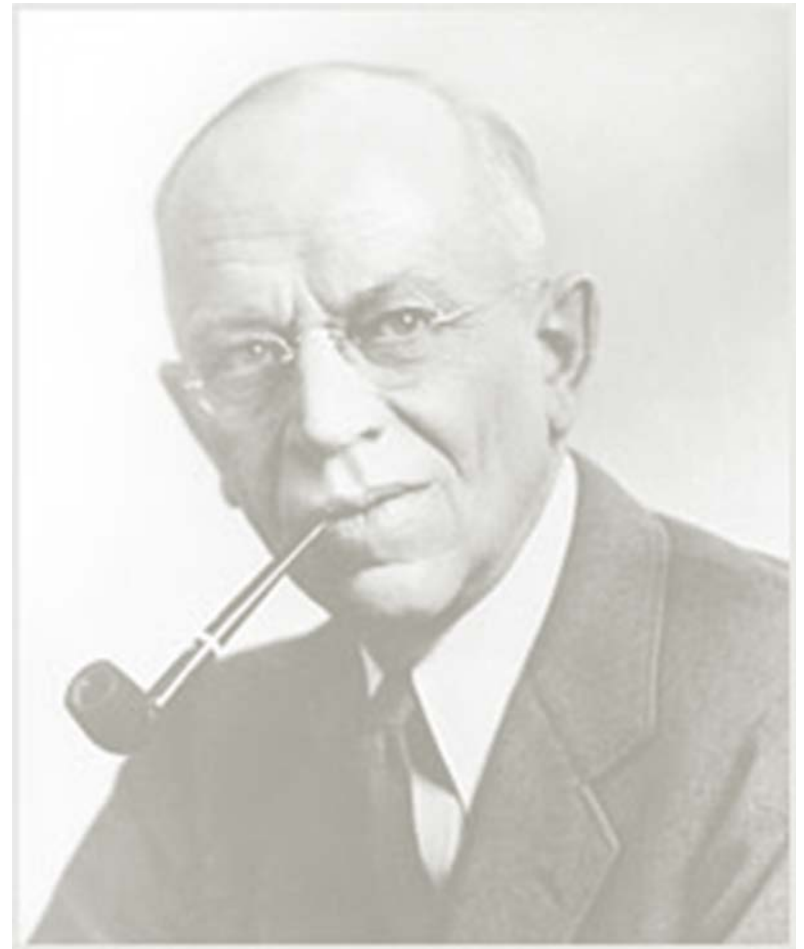
What did Leopold Actually Write?

- “Abundance of non-mobile wild life requiring two or more types, appears, in short, to depend on the degree of **interspersion** of those types, because this determines the length of the **edges** of those types, and thus in turn their vegetative richness and simultaneous availability.”



What did Leopold Actually Write?

- ...as the law of **dispersion**: “The potential density of game of low radius requiring two or more habitat types is, within ordinary limits, proportional to the **sum of the type peripheries.**”



What Leopold Meant

- We can deduce a more modern definition of what Leopold meant by interspersions: the spatial intermixing of different patch types (McGarigal and Marks 1995)

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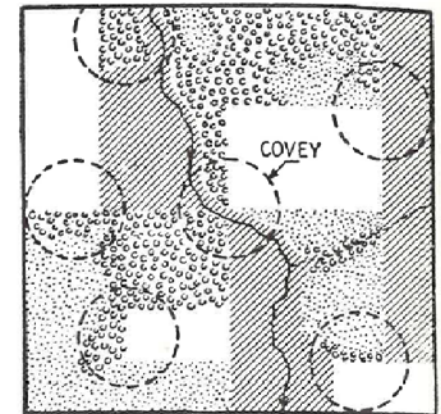
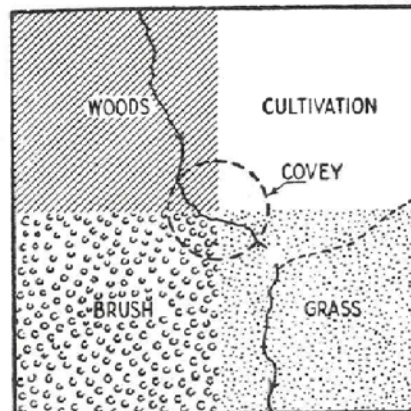
GAME MANAGEMENT

FIG. 9

INTERSPERSION OF TYPES - RELATION TO MOBILITY & DENSITY OF QUAIL
(SAME TYPES AND SAME TOTAL AREA OF EACH)

A: Poor Interspersion (1 Covey)

B: Good Interspersion (6 Coveys)



What Leopold Did Not Write

- “Principle of Edge” – not used by Leopold
 - Leopold wrote “*Game as an edge effect*”
- “*Principle of Edge*” coined by Guthery and Bingham (1992)

Wildl. Soc. Bull. 20:340–344, 1992

“COMMENTS . . .”

ON LEOPOLD'S PRINCIPLE OF EDGE

FRED S. GUTHERY, *Caesar Kleberg Wildlife Research Institute, Texas A&I University, Kingsville, TX 78363*

RALPH L. BINGHAM, *Caesar Kleberg Wildlife Research Institute, Texas A&I University, Kingsville, TX 78363*

Leopold's (1933:132) principle of edge, considered an enduring precept of wildlife habitat management (Kelker 1964), has “grown into a theorem by usage rather than by more scientific methods” (Giles 1978:139). In other words, attempts to disprove the principle have been few. The merit of a hypothesis or theory increases as it withstands repeated attempts at disproof (Bronowski 1973:240).

Further, the principle has become nebulous because interpretations differ among biologists. Robinson and Bolen (1984:82) reported that “Leopold . . . felt that density of wildlife is directly proportional to the amount of interspersed or ‘edge’ available in habitat.” Barnes et al. (1991:189) had a different concept: “Generally, the greater the number of habitat types or habitat boundaries (edges) present with an area, the greater the diversity and abundance of wildlife.” These recapitulations of the principle do not convey the precise meaning intended by Leopold, in part because they ignore constraints he imposed.

In short, the principle of edge is a somewhat vague, largely untested concept, and we thought the time appropriate to reexamine Leopold's (1933:132) original thinking. Our arguments relate to high-contrast edge, such as that created by openings in a mature woody-plant community. We will argue that the basic assumption of the principle is tenable, but that the original concept is too narrow. We attempt

to define what Leopold meant by the qualifying phrase, “within ordinary limits,” and we show that the principle breaks down under circumstances beyond ordinary limits. We hope these musings will stimulate researchers to challenge the principle of edge and managers to become more cautious in its application.

THE PRINCIPLE OF EDGE

General

Leopold (1933:132) expressed the principle as follows: “The potential density of game of low radius requiring [2] or more types is, within ordinary limits, proportional to the sum of the type peripheries.” In equation form, the principle is

$$D = kS,$$

given low radius, ≥ 2 required types, and ordinary limits where

D = potential density,

k = a constant of proportionality, and

S = the sum of type peripheries.

The principle as stated applies to edge-obligate species because there is no intercept, i.e., $D = 0$ if $S = 0$. To make the principle more general, an intercept could be added (Fig. 1):

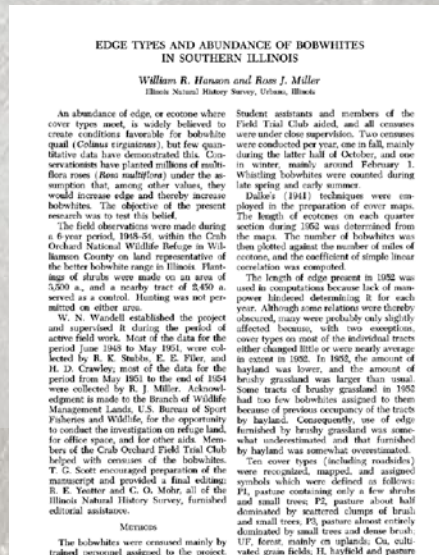
$$D = a + kS,$$

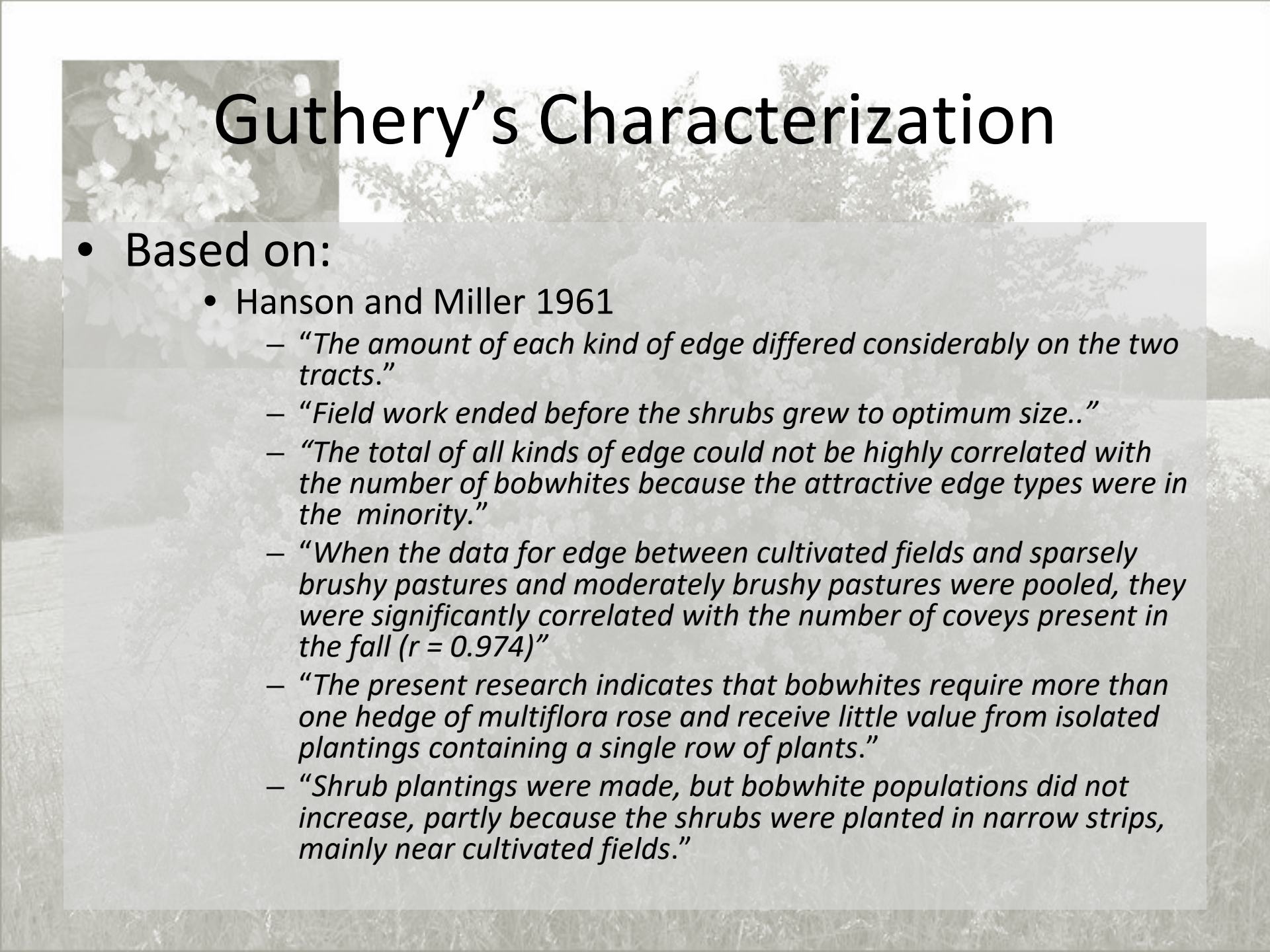
Guthery's Characterization

- *“Principle of Edge”*
 - High contrast edge
 - *“..created by openings in mature woody plant communities.”*
 - *“Bobwhite abundance should be related positively and linearly to the density of woody edge if Leopold's law of dispersion holds.”*
 - Redundant edge = *“within ordinary limits”*

Guthery's Characterization

- Based on....
 - Hanson and Miller 1961
 - Guthery and Bingham 1992
 - “Hanson and Miller (1961) observed this situation in Illinois, where creation of additional edge had no effect on northern bobwhite density.”



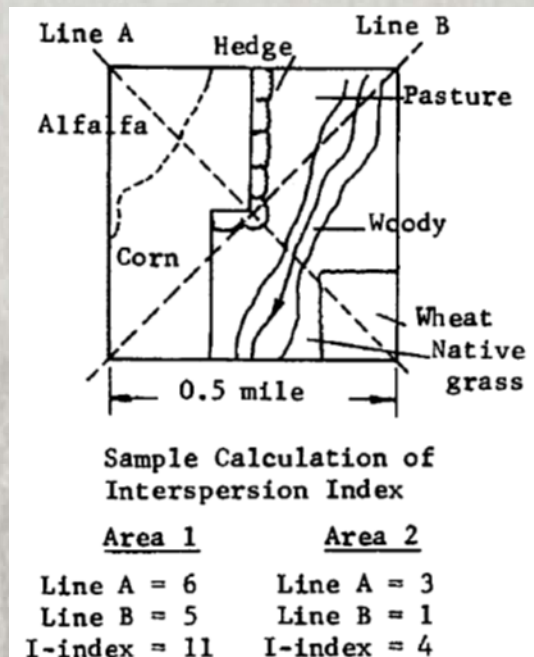


Guthery's Characterization

- Based on:
 - Hanson and Miller 1961
 - *“The amount of each kind of edge differed considerably on the two tracts.”*
 - *“Field work ended before the shrubs grew to optimum size..”*
 - *“The total of all kinds of edge could not be highly correlated with the number of bobwhites because the attractive edge types were in the minority.”*
 - *“When the data for edge between cultivated fields and sparsely brushy pastures and moderately brushy pastures were pooled, they were significantly correlated with the number of coveys present in the fall ($r = 0.974$)”*
 - *“The present research indicates that bobwhites require more than one hedge of multiflora rose and receive little value from isolated plantings containing a single row of plants.”*
 - *“Shrub plantings were made, but bobwhite populations did not increase, partly because the shrubs were planted in narrow strips, mainly near cultivated fields.”*

Guthery's Characterization

- Based on:
 - Baxter and Wolfe 1972
 - Guthery 1997
 - “On 3 areas in Nebraska, there was a weak association between edge density and bobwhite abundance (Baxter and Wolfe 1972).”



Guthery's Characterization

- Based on:
 - Baxter and Wolfe 1972

Table 3. Comparisons of preseason inventories of bobwhite quail (4-year average number of calls per stop) and interspersions indices.

Characteristics	Cass	Otoe	Pawnee
Mean number of calls per stop (1964-1967)	1.88	2.50	5.14
Interspersions index	404	631	984

of habitat. The relationship between the interspersions and whistle-call indices was tested by linear correlation. The calculated r value of 0.976 indicated a significant correlation between quail numbers and the frequency of cover type change.

Guthery's Characterization

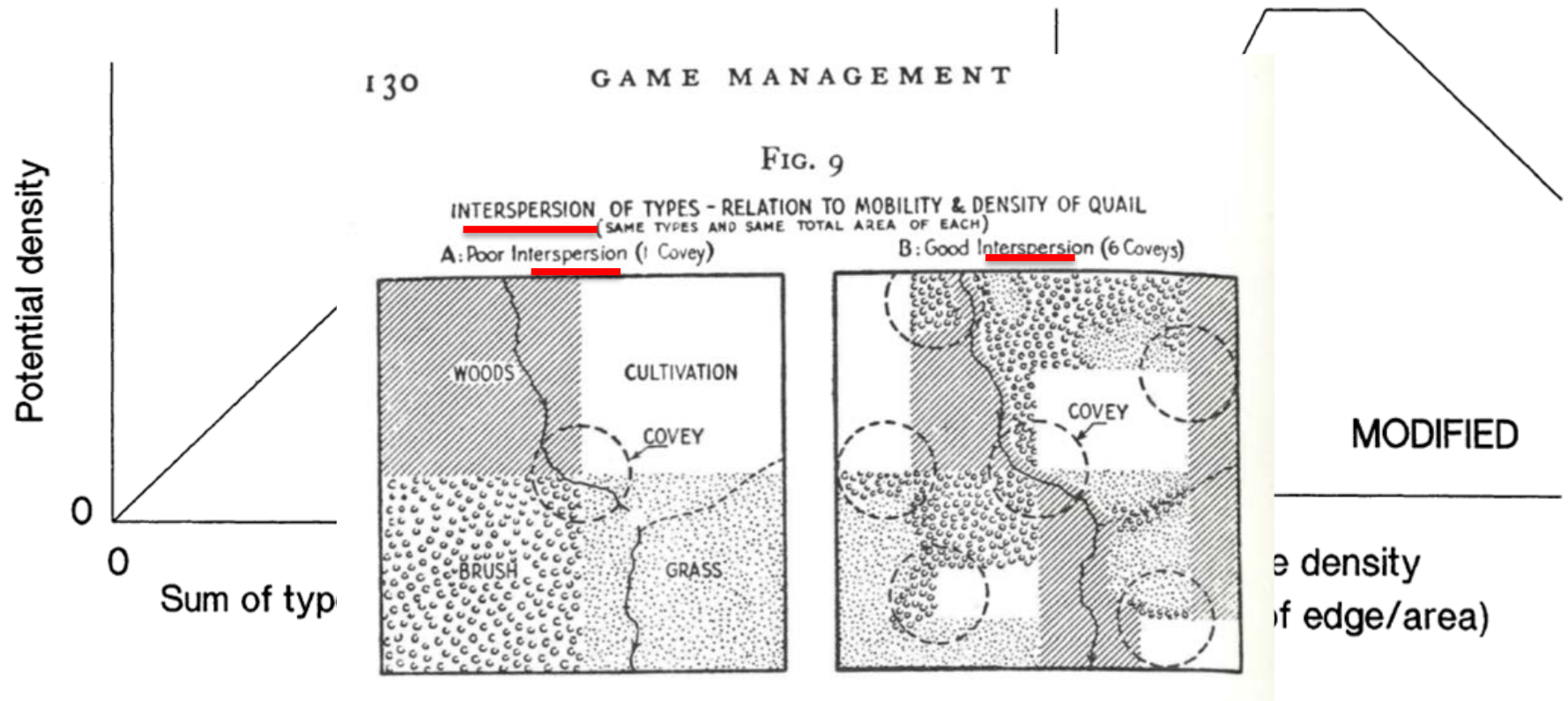


Fig. 1. Graphic portrayal of the principle of edge as originally developed by Leopold (1933:132) and as modified.

Guthery's Characterization

- Biologically Redundant Edge
 - Assumption regarding where a landscape falls on this curve?
 - Risk in assuming a landscape is already at a point of redundancy

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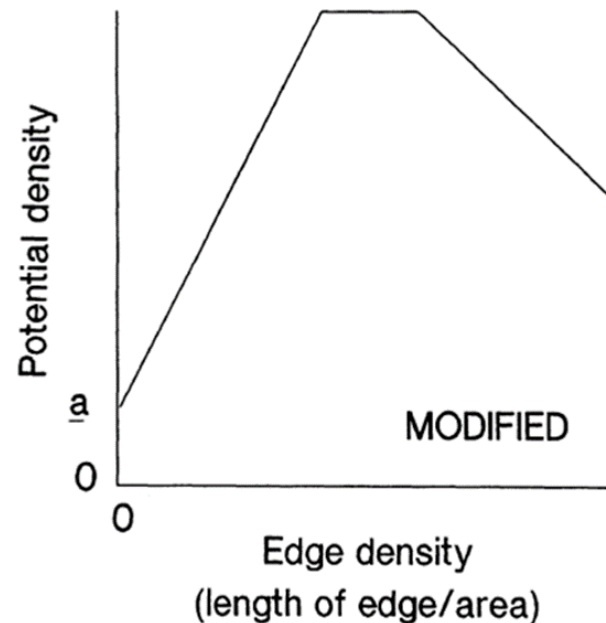
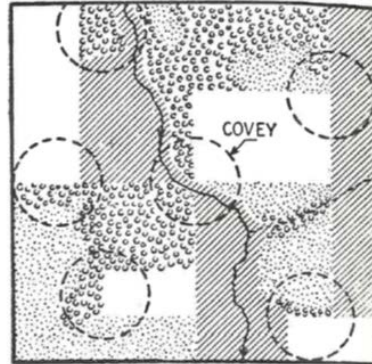
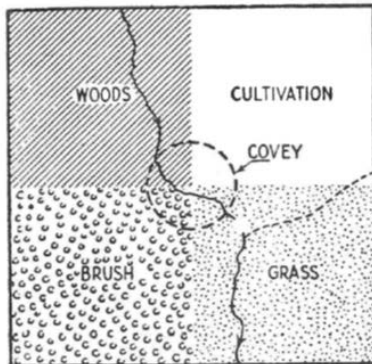
GAME MANAGEMENT

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A: Poor Interspersion (1 Covey)

B: Good Interspersion (6 Coveys)



Misconceptions

- “Linear mileage of type edges available in any block of range, is, as a matter of geometry, proportional to the degree of interspersion.”
 - ‘proportional to’...not equal to!



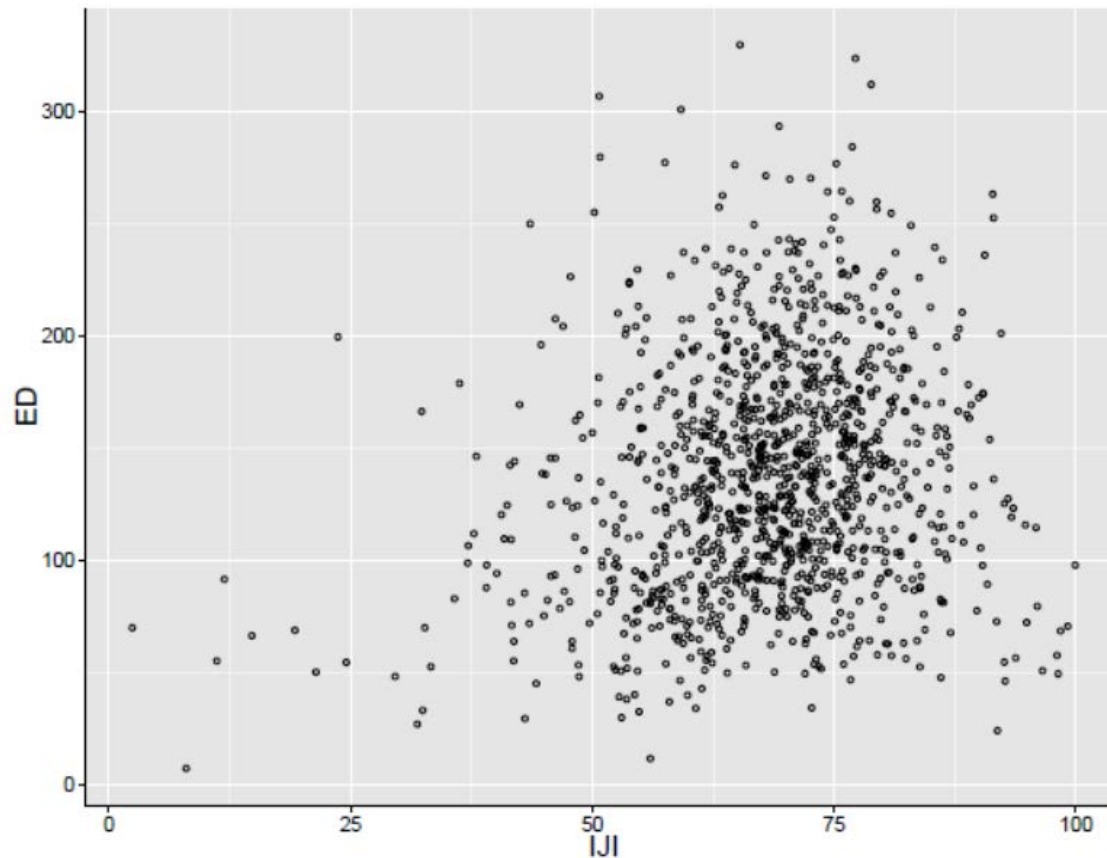
Misconceptions

- Leopold was referring to '*high contrast*' edge
- Leopold was referring to just two 'types'



Misconceptions

- Edge density and Interspersion are synonymous

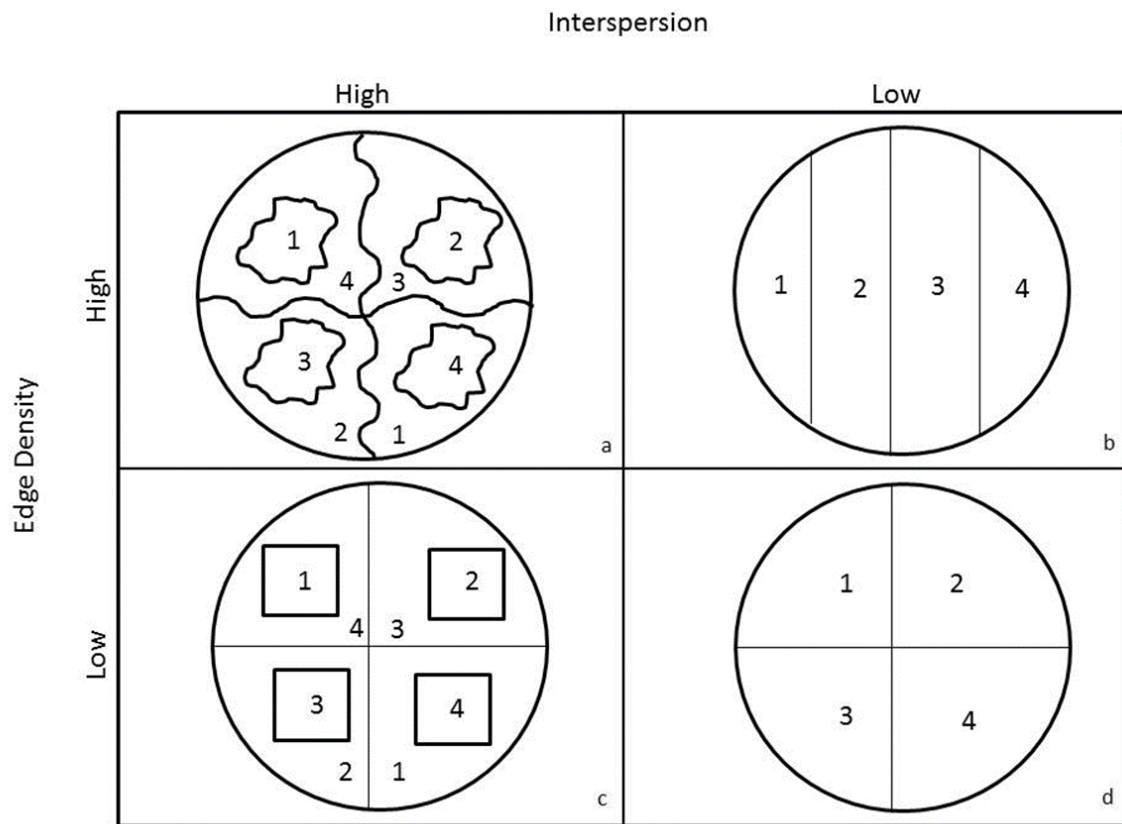


Misconceptions

- Edge density and Interspersion are synonymous
 - Edge density is the amount of border between two patches
 - but for a given edge density there could be 2 or multiple patches in a variety of configurations (i.e., clustered or dispersed)
 - Edge density can increase without increasing interspersion

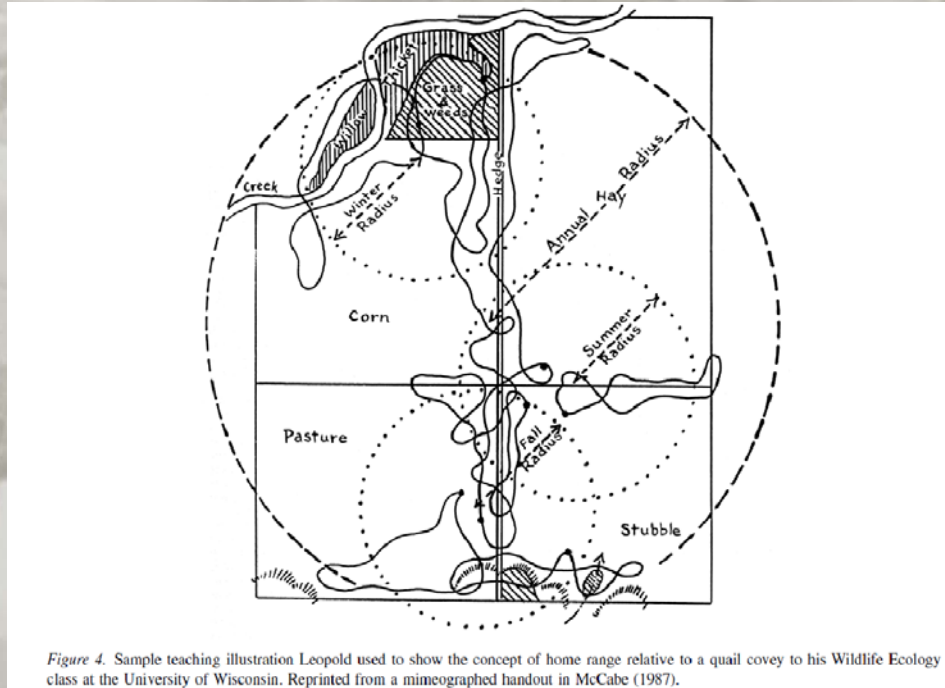
Misconceptions

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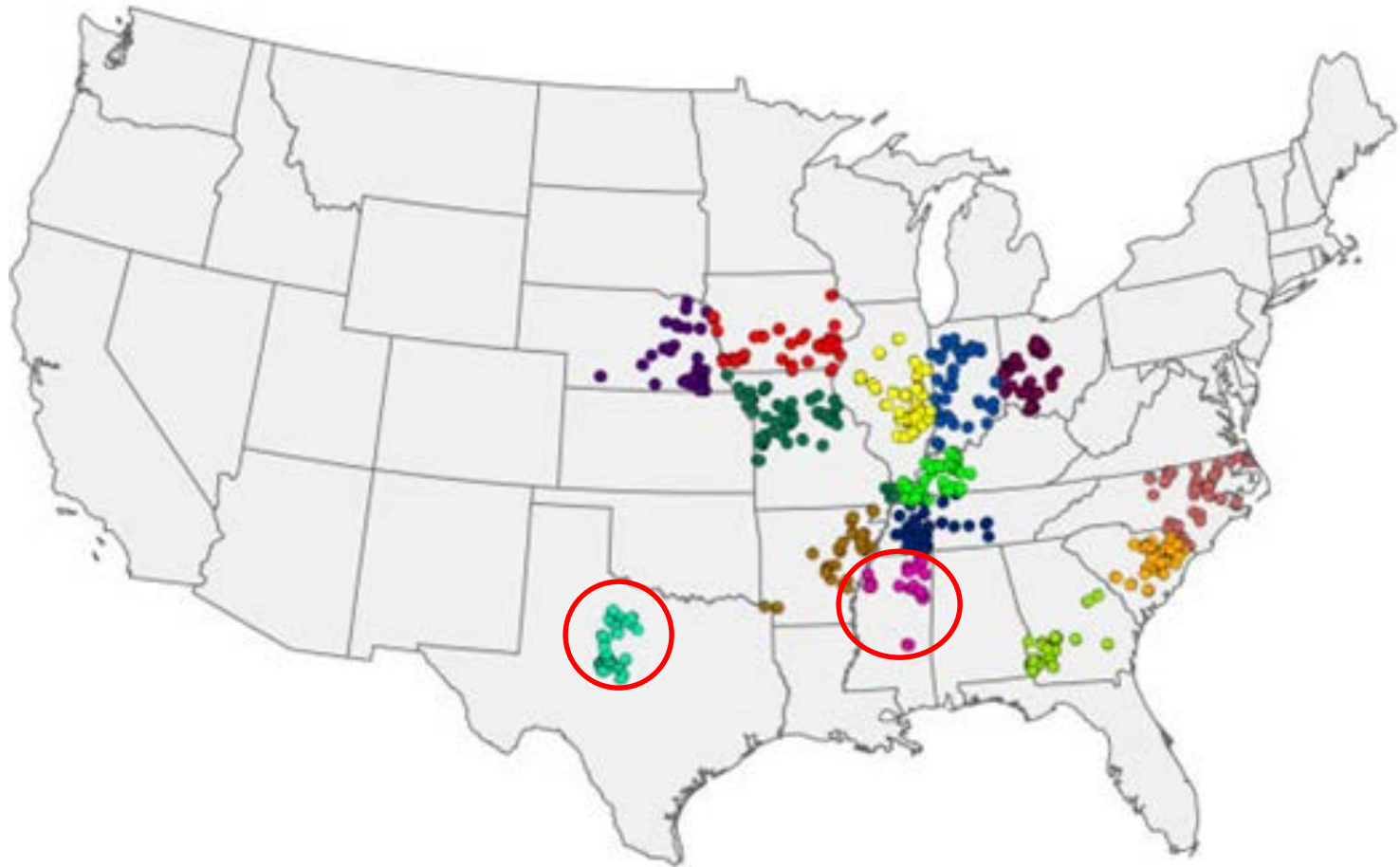
Misconceptions

- *“...Leopold did not simplify this relationship into an assertion that more edge equals more game.”*
 - J. Silbenagel Landscape Ecology 18:635-646 - 2003



Results from Mississippi and Texas

Distribution of CP-33 Monitoring Survey Points

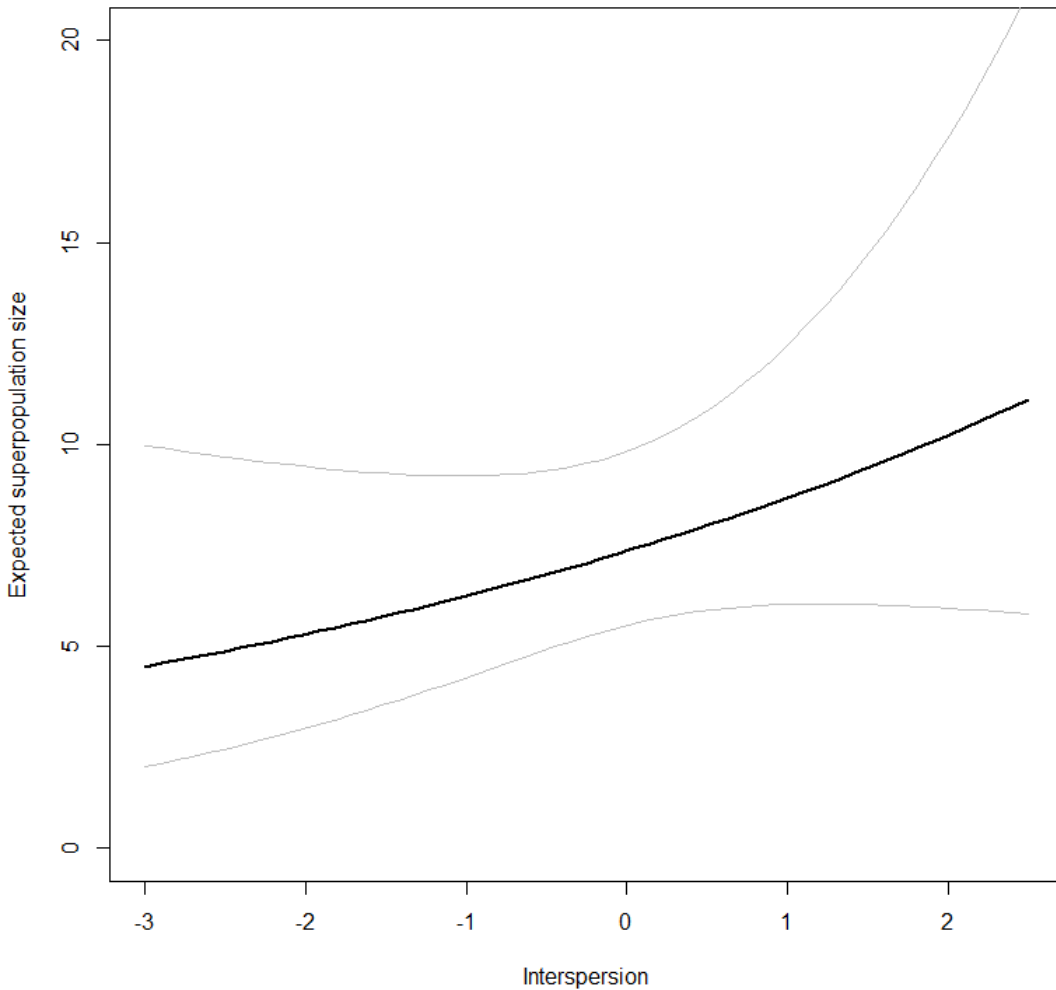


Results from Mississippi and Texas

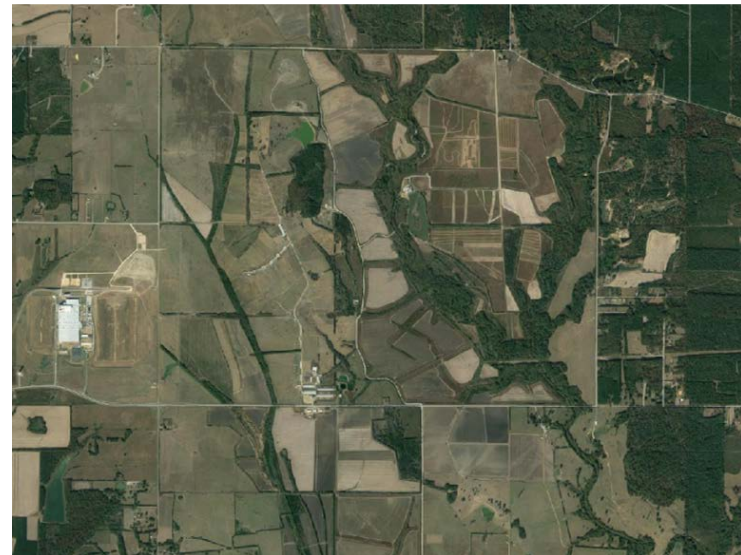
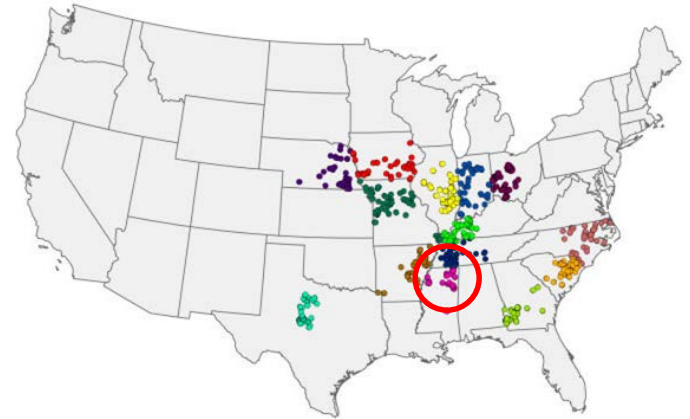
- Utilized a multiple-season occupancy modeling approach
- Following Dail and Madsen 2011:
 - Open population assumed
 - Temporary immigration/emigration
 - Allows for imperfect detection
 - Pollock's Robust Design..



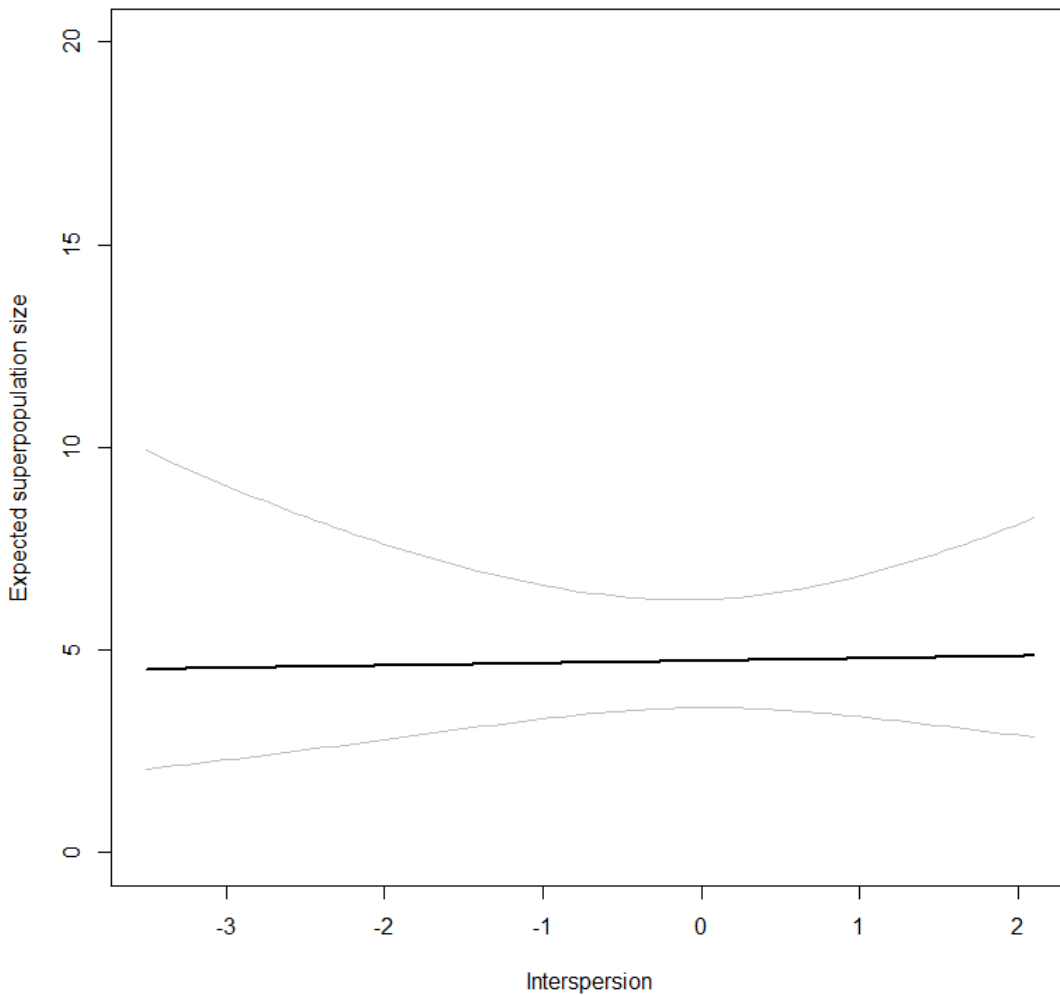
Results from Mississippi



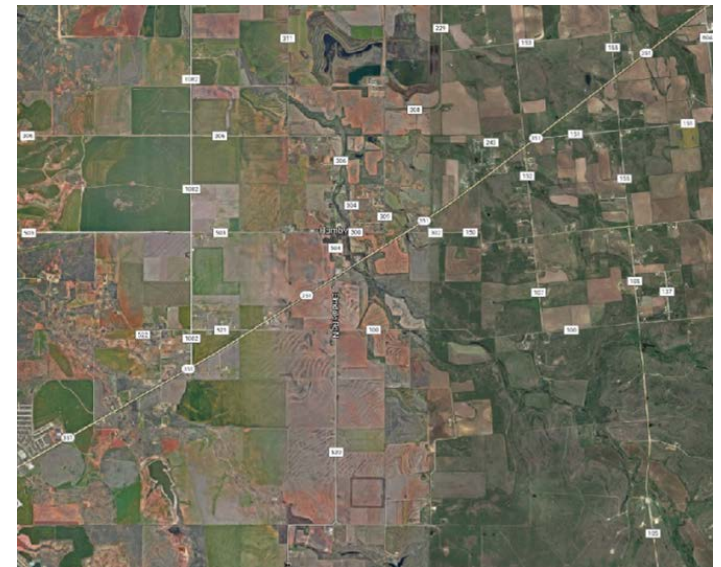
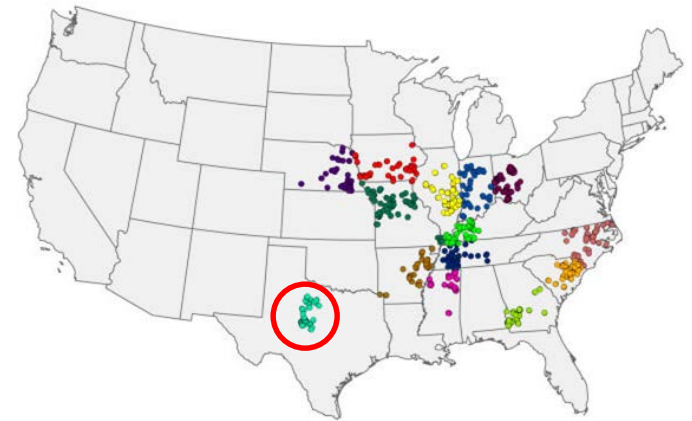
Distribution of CP-33 Monitoring Survey Points



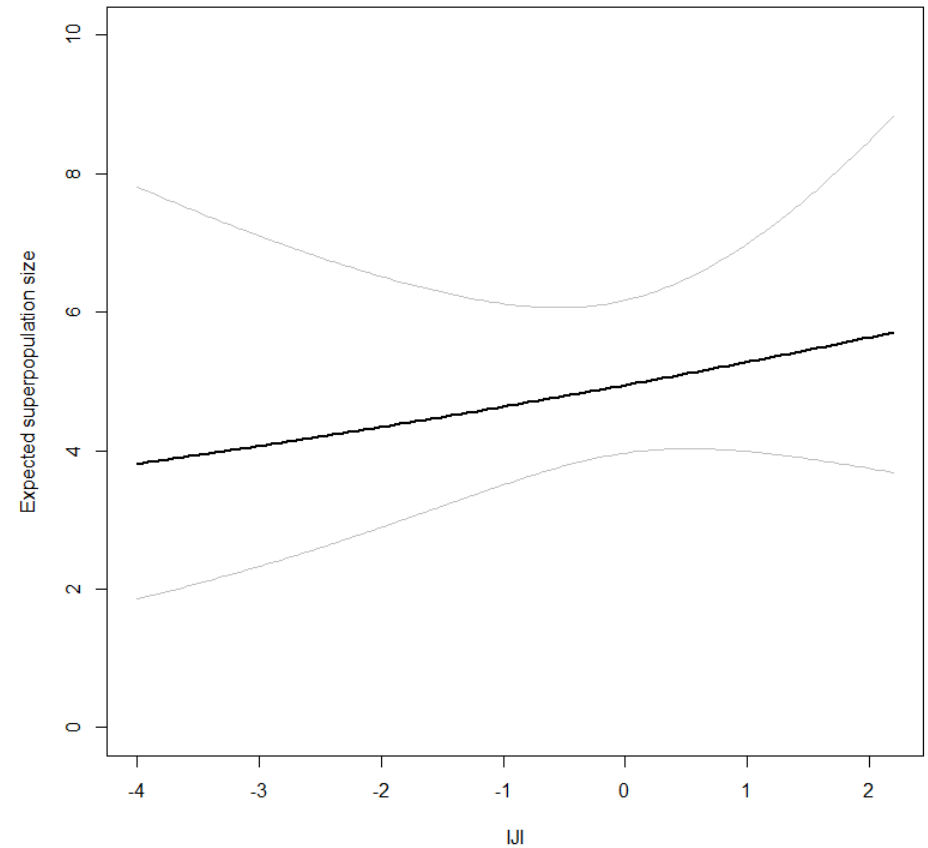
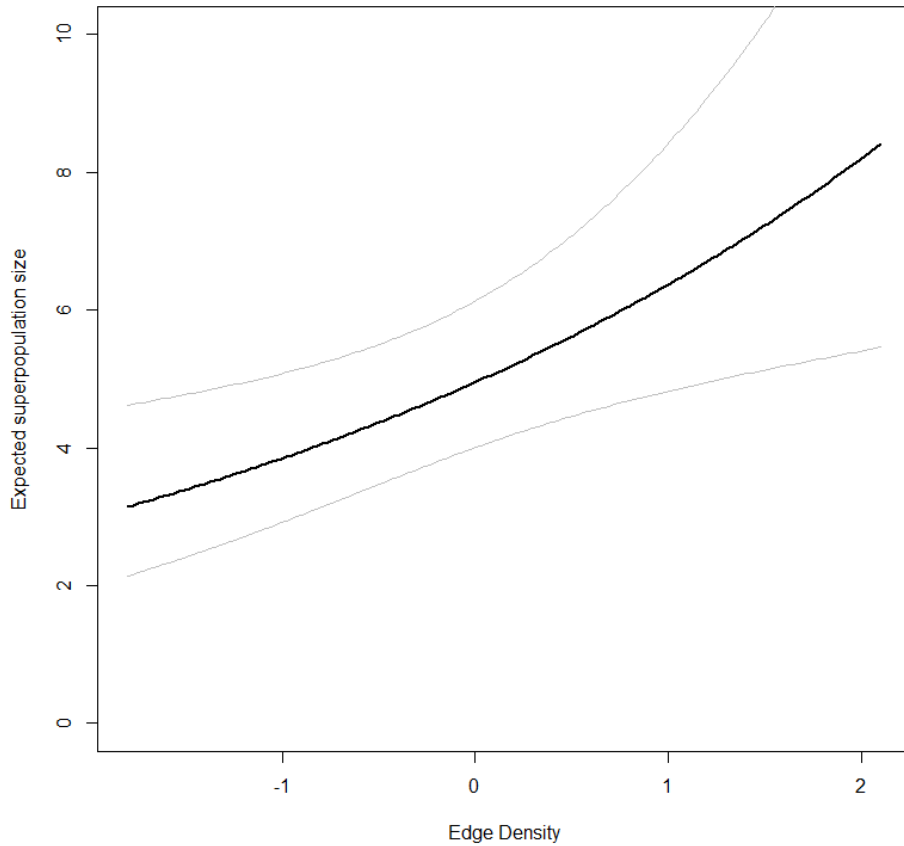
Results from Texas



Distribution of CP-33 Monitoring Survey Points



Results from Mississippi and Texas Combined



Results from Texas and Mississippi

- Different landscapes
- Differences in edge detectability and biological significance



Rangeland



Agricultural

Musings

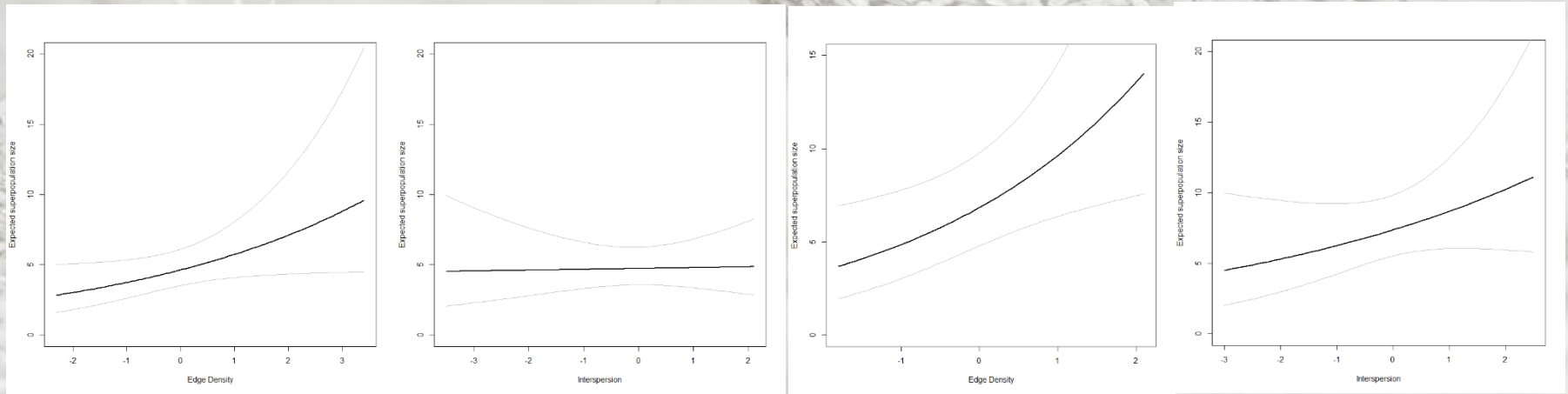
- The Law of Interspersion is NOT the Principle of Edge
 - We contend that
 - Leopold was referring to interspersion
 - BUT, lacked the understanding of the potential disparity between the two terms
 - The field of Landscape Ecology had not yet been developed
- The Law of Interspersion and the Principle of Edge are two different ecological constructs

Musings

- Guthery and Bingham's articulate argument has limited the application of the Law of Interspersion in the field of wildlife ecology.
- The time has come to reevaluate both Leopold's central premise and Guthery and Bingham's reformulation of the law of interspersion and the principle of edge.

Future Directions

- Guthery et al. 2001
 - *“The law can be resurrected only if other scientists can demonstrate that the counter instances observed, both theoretical and empirical are invalid.”*



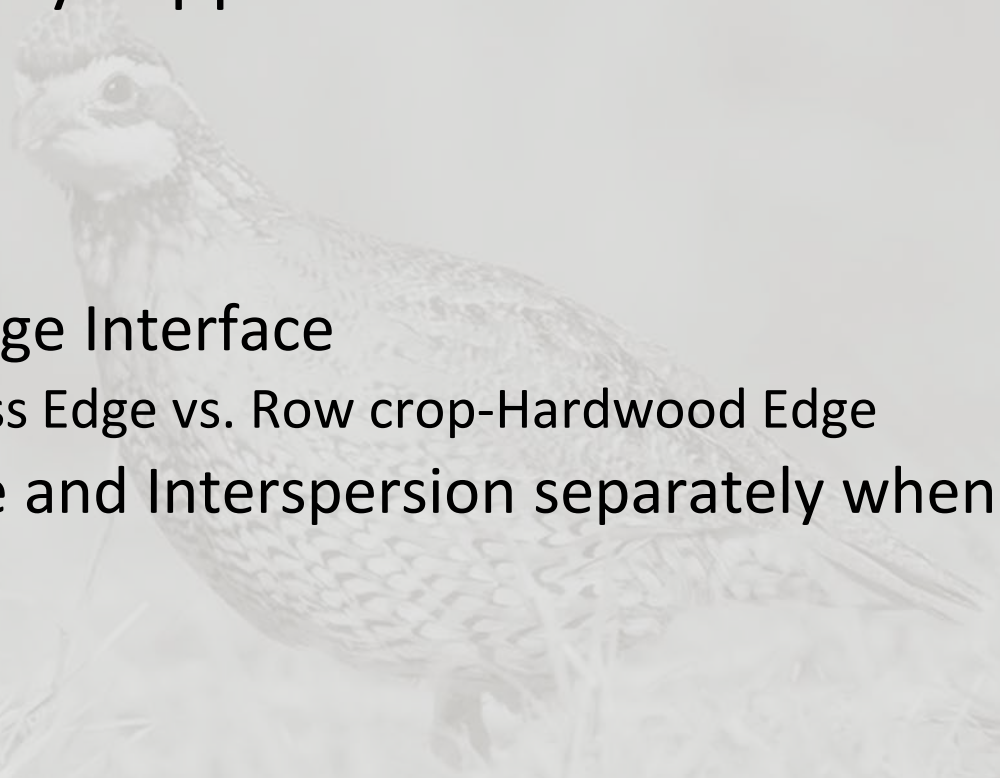
Future Directions

- Changes in Wildlife Communities Near Edges – Richard H. Yarhner – 1988
 - *“In short, edges are not created equal, and, hence their edge effects for wildlife should not be expected to be equal.”*



Future Directions

- More theoretically supported research
 - Well designed
 - Manipulative
 - Long term
 - Examine the Edge Interface
 - Row crop-Grass Edge vs. Row crop-Hardwood Edge
 - Examining Edge and Interspersion separately when appropriate



Acknowledgments

