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ABSTRACT

Powerful ideas in quailology affect thinking over generations, even if the ideas are wrong. I discuss great ideas put forth by Aldo Leopold, Herbert Lee Stoddard, and Paul Lester Errington and comment on aspects of their personalities. Leopold, an extraordinarily good father, posited the Law of Dispersion (Interspersion), which became known as the Principle of Edge. The Law is a tautology that can be paraphrased 'edge-obligate animals require edge.' Leopold observed the 'law' held 'within ordinary limits,' which he did not define but which could mean 'within compositionally simple landscapes.' As a child, Stoddard, who dropped out of high school to support his family, recognized the value of fire in northern bobwhite (*Colinus virginianus*) habitat management in the Southeast; later he came to see tenant farming (patchwork agriculture) set up conditions favorable to northern bobwhites. Stoddard was given to after-the-fact hypothesis formulation (retroduction) on the causes of events he observed. Through this logically weak process he bequeathed many 'facts' that are really untested hypotheses. Errington, an apparent loner who survived polio as a child, had 2 great ideas. The Threshold of Security was a fairly constant spring density which implied harvest up to a certain level is fully compensatory (doomed-surplus model). The Principle of Inversity implies that relative productivity declines as breeding density increases. Errington's own work refuted the doomed-surplus model because he could not have simultaneously observed a constant breeding population and inversity, which requires a variable breeding population. These great founding ideas, although not without flaw, arose through observation of nature and thought, not through null hypothesis significance testing and model selection.

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INTRODUCTION

> Most theoretical breakthroughs in ecology have come from thinkers accomplished in field natural history.—Thomas L. Fleischner (2005:6).

My library contains *Six Great Ideas* by Mortimer J. Adler (1981). Adler's great ideas are from philosophy: truth, goodness, beauty, liberty, equality, and justice. He categorizes great ideas as those "basic and indispensable to understanding ourselves, our society, and the world in which we live" (1981:3) and suggests such ideas constitute "the vocabulary of everyone's thought."

Great ideas in northern bobwhite management are, of course, blind hairless puppies in comparison with the great ideas of human philosophy. However, these ideas help us better understand and appreciate our world. The great ideas affect our thinking over human generations, even if they are wrong. If they are wrong, flaws in thinking obviously have been discovered and perhaps a greater idea has emerged. Indeed, science is all about the birthing of greater ideas from lesser ones.

I discuss the great ideas put forth by what low-handicap colinologists call the Big Three: Aldo Leopold (1886–1948), Herbert Lee Stoddard (1898–1968), and Paul Lester Errington (1902–1962). (By twist of fate the lives of these intellectual giants intertwined in Wisconsin.) Their great ideas have to do with the Law of Interspersion and basic theory of wildlife management; research, prescribed burning, and cultural aspects of landscapes; and the nature of harvest and production in bobwhite populations. I will inject some personal and career tidbits about each that will help us appreciate that they were, indeed, mortals. I conclude with a brief comment on their *modus operandi* in comparison with obsessive use of significance testing and model selection today.

LEOPOLD AND THE LAW OF DISPERSION

Aldo the Father

Aldo Leopold was a wonderful dad. "He treated us with considerable dignity," said A. Starker Leopold, the eldest child (Meine 1988:292). "Aldo inevitably began conversations by asking the children what they thought about this or that. At the dinner table, he would routinely inquire of each of the five [children] in turn, 'What happened today in your life that was interesting?'" He and his wife, Estella, also gave the children responsibility and trust. Each of his children had exemplary careers and three were elected to the National Academy of Science.

Forgive me this bit of sentimentalism on Leopold. I simply believe it is nice that a busy man of some import would listen to his children, and I think we should know this about him. Such an anecdote sits nicely upon the

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palate like the after effects of spice from a gourmet soup. This also explains how his personality might have intensified the esteem in which he was held by contemporaries and future observers.

Perhaps this reference to being a father also is appropriate because he is regarded as the father of *game* management. Indeed, he published *Game Management* in 1933. This book was a compendium on the natural history and management principles of game animals. Leopold was fascinated with all the wild plants and animals he encountered, not just game, as apparent from his essays in *A Sand County Almanac* (1949). His campaigns for wilderness preservation also attest to this fact.

Leopold was born to Carl and Clara (Starker) Leopold in Burlington, Iowa, on 11 January 1887 (Meine 1988). His parents were first cousins (cross cousins). This is not unprecedented among great biologists as Charles and Emma Darwin were first cousins. Neither was marriage of cousins unusual in late 19th century America.

His father, Carl, kindled Leopold's interest in the out-of-doors through field excursions with the family, hunting, and fishing. Leopold began hunting at about 13 years of age (Meine 1988). He also did considerable hiking whenever he had the opportunity, which was often; being a child of privilege, Leopold did not have to work for wages until he graduated from college.

The Principle of Edge

Hunting and otherwise tramping about the hinterlands provided diverse observations for Leopold's mind to stir and ponder. These observations led to inductions about the workings of nature. His most famous induction is what he called the Law of Interspersion (Leopold 1933:131). He also called it the Law of Dispersion (1933:132). Today, we know it as the Principle of Edge.

> The potential density of game of low radius requiring two or more types is, within ordinary limits, proportional to the sum of the type peripheries.—Aldo Leopold 1933:132.

The phrase 'low radius' means an animal with low mobility (travels short distances in daily activities) such as bobwhites or cottontails (*Sylvilagus* sp.). 'Type' means 'cover type' such as wheat field, prairie, brushland, and others. Leopold did not explain what he meant by the phrase, 'within ordinary limits' and we will return to this phrase.

The law may be stated mathematically as:

$$D = k\sum P_i = k(P_1 + P_2 + \ldots + P_n),$$

which reads 'potential density (D) is proportional to (k) the sum of type peripheries ($\sum P_i$)'. The equation reveals an oddity: 'potential density' (no./area) implies that some area (length and width) is under consideration but $\sum P_i$ is a measure of length. That leaves the units for the constant of proportionality in question. Let us suppose, however, that Leopold intended to use edge density ($\sum P_i/A$; edge per area) (Guthery and Bingham 1992). The corrected equation then becomes

$$D = (k/A)\sum P_i = (k/A)(P_1 + P_2 + \ldots + P_n).$$

The units for the constant of proportionality then become no./edge and we have the Principle of Edge in words as:

$$\text{no./area} = (\text{no./edge})(\text{edge/area}).$$

Thus the Principle of Edge is mathematically tautological (all equations are) because edge cancels out on the right side of the equation and we find:

$$\text{no./area} = \text{no./area}.$$

The principle is verbally tautological, too: Leopold defined an edge-obligate animal and asserted it occurs with edge. This could be stated, 'animals that require edge live near edge.'

The corrected principle, when expressed as an equation, reveals a strong assumption. First, consider that if an area has n different cover types and we are interested in 2-type edges (e.g., prairie-forest edge), there potentially are a maximum of $n!/(2!(n-2)!)$ unique 2-type edges. (There could be fewer edge types depending on how cover types are dispersed.) If an area has 5 cover types, for example, there are potentially $5!/(2!(5\text{-}2)!) = 10$ 2-type edges. By virtue of the *constant* of proportionality, k, in the corrected principle, each edge type is *assumed* to be of identical value to wildlife. When the assumption fails, the principle becomes:

$$D = (1/A)\sum k_i P_i = (1/A)(k_1 P_1 + k_2 P_2 + \ldots + k_n P_n),$$

where k_i is no./edge for edge type i. One supposes that, given the above expression of the Principle of Edge, the principle would be virtually useless in complex landscapes (many cover types). The reason is the value of any 2-type edge could be hopelessly confounded with the value of any other 2-type edge. Moreover, given what we know about habitat use (i.e., an animal uses different cover types to fulfill different needs) it is difficult to imagine that all 2-type edges are of identical value to the animal in different edge contexts.

Perhaps the hopeless confounding of edge values in complex landscapes was a consideration for Leopold's qualifier, 'within ordinary limits,' but there are other possibilities. Weather catastrophes could make unlikely or obscure any relation between abundance and edge, at least in the near term (J. H. Shaw, Department of Natural Resource Ecology and Management, Oklahoma State University, personal communication). It is mathematically possible to create an infinite amount of edge on a 3-×-5 note card and one could play the same kind of mind games on a square kilometer or any area. Obviously, there would be no relation between animal abundance and edge as edge density increases without bound leading to redundant edge (Guthery and Bingham 1992).

Another consideration is a property of cover configurations called 'slack'; the property implies that different amounts and arrangements of cover types can be of equal value to a wildlife population (Guthery 1999). To the extent that slack operates, the Principle of Edge is inapplicable because abundance stays the same as amount of edge varies.

Guthery and Bingham (1992) reasoned that 'within ordinary limits' might entail a maximum possible density. Indeed, density is problematic in Leopold's rendition of the Principle of Edge because standardized density (e.g., no./ha) may have little variation from low to high. Leopold probably was thinking of density as a synonym for population size (N); Errington (1945) used the words as synonyms. Any statement of population size is a statement of density because the population is implicitly confined to some area of interest. If Leopold used density as a homologue of population size, his principle is more reasonable if the identified problems are corrected. If, however, Leopold was implying standardized density (no./unit area) we have mystery. Suppose all usable space on an area is occupied (maximum population size) and we add edge. Density (and abundance) would increase under a strict interpretation of the Principle of Edge. This is contrary to empirical reason: what mysterious force would cause abundance to increase with the addition of edge that is unnecessary from the standpoint of usable space?

These concerns could explain individually or as a group why Leopold constrained his principle to ordinary limits. I suspect he had a hunch the principle would work only on simple landscapes (few cover types). 'Within ordinary limits' perhaps means 'given relatively simple arrangements of a few cover types on a landscape.'

Edge vs. Usable Space

Guthery (1997) developed what he called the usable space 'hypothesis', which is a generalization of the Principle of Edge. The 'hypothesis' may be expressed as

$$N = pDA,$$

where

$N =$ population size on an area,
$p =$ the proportion of the area that is usable by quail,
$D =$ average density in usable space at some time of interest, and
$A =$ the size of the area (e.g., ha).

The quantity of usable space is pA. The 'hypothesis' is in fact a tautology. Letting $p = 1$ (all space usable) we have:

$$\text{number} = (\text{number/area})(\text{area}) = \text{number}.$$

Because the Principle of Edge has an implicit statement of area (Guthery and Bingham 1992), it is contained in the usable space hypothesis. If l is the length of edge and w is its effective width (usable space $= lw$), it can be shown by algebra that $lw = pA$ and by substitution:

$$N = Dlw,$$

which contains edge (l). However, $N = pDA$ is a better conceptual model because it deals with quandaries such as redundant edge and 'slack' (different amounts of edge have the same value to a wildlife population).

Leopold's Principle of Edge is now a conceptual debacle, but his philosophical contributions to wildlife conservation are properly treated with reverence. He was a champion of wilderness preservation throughout his career. His writing gave conservation a moral compass. *A Sand County Almanac* is regarded by many as the bible of the conservation movement (McCullough No Date).

Leopold noticed smoke coming from the direction of a neighbor's house on 21 April 1948 (Meine 1988). He, his wife, and his daughter (Estella Jr.) gathered up fire-fighting tools and went to help extinguish the fire. Leopold died of a heart attack while fighting the fire.

''There were no witnesses to [his] final moments. . ..He apparently set down the full [water] pump, lay down on his back, rested his head on a clump of grass, and folded his hands across his chest. The attack did not subside. The fire, still alive but weakened in intensity, swept lightly over his body'' (Meine 1988:520).

STODDARD AND TENANT FARMING

The Improbable Rise to Eminence

A remarkable absence in Herbert L. Stoddard's (1931) classic, *The Bobwhite Quail: Its Habits, Preservation and Increase*, is a section listing references. Technical articles on bobwhites were largely non-existent in the 1920s. In contrast, *Texas Quails: Ecology and Management* (Brennan 2007) cites about 1,000 different articles.

The absence of literature was a bane to Stoddard because "there was little precedent to assist in the planning or execution of the project" (Stoddard 1931: xxi). However, a paucity of knowledge was also a blessing in that all the information gathered was original.

Stoddard was in some ways ill-qualified by background and education to take on leadership of the Cooperative Quail Investigation. He was born in Rockford, Illinois on 24 February 1889. His father was an intensely religious person who taught mathematics and penmanship at Stoddard-Winans Business College in Rockford (Stoddard 1969). His father died when he was 5 weeks old. His mother remarried and Louis S. Flint, the stepfather, moved the family to Florida in 1893. Flint had no talent for 'the earning of a dollar,' said Stoddard and the family returned to Rockford in poverty in 1900.

Stoddard dropped out of school at the age of 15 in 1905 owing to 'the never-ending shortage of money' in his family (Stoddard 1969). He went to work near his Grandfather Stoddard's farm near Prairie du Sac, Wisconsin. (This locale would later play prominently in Paul L. Errington's career.) The young Stoddard worked 15 hours a day for $15 a month.

Stoddard worked as a taxidermist for the Milwaukee Public Museum and the Field Museum of Natural History in Chicago during 1910–1924. World War I interrupted this work and he was stationed near Bordeaux, France, when the war ended in November 1918. Stoddard saw no combat duty. "I left the service with a clearer understanding of myself and my lifework,'' Stoddard (1969:137) averred.

The Cooperative Quail Investigation

Early in the 20th century, declining bobwhite populations on plantations in the general vicinity of Thomasville, Georgia, and Tallahassee, Florida, prompted a meeting of wealthy landowners at the Links Club in New York City (Stoddard 1931). These preserve owners decided research might help identify and resolve the problems of quail. (This is one of the earliest examples in America where research was invoked to solve a conservation problem. Leopold [1948] also was an early advocate of research.) They affiliated with the U.S. Bureau of Biological survey to administer the project. The landowners anteed up $46,250.52 to fund the project.

The objectives were to study "all phases of the life history of the bobwhite, with special emphasis on the character and improvement of the food supply and general environment, and on the factors of mortality as represented by predatory enemies, the elements, parasites, diseases, and regulated and unregulated shooting" (Stoddard 1931: xxiii). The project started in March 1924 and ended in June 1929.

Fire and Bobwhite Management

Besides being the first wildlife monograph of American origin and a lode of descriptive natural history information, *The Bobwhite Quail* presented 2 great ideas. The first was use of fire in habitat management.

Stoddard's insight on the role and value of fire was a product of his youth in Florida, not of his work in the Cooperative Quail Investigation (Stoddard 1969:180). He wrote that fire had 3 main positive effects for bobwhites: increased food supplies, reduced or eliminated jungle-like aggregations of deciduous shrubs and high biomass aggregations of forbs and grasses (non-usable space), and sterilized the countryside for ticks, chiggers, and certain intestinal parasites. Today we would question the value of increased food supplies and sterilization for parasites but agree with the creation of usable space as the key factor in increasing bobwhites (Guthery 1997).

Stoddard (1931:411) recognized that *fire is not imperative for bobwhite habitat management*: "The cover on many upland preserves can be kept in shape . . . largely with the use of tractors and plow-harrows, but the expense is greater [than fire] and in many cases might be prohibitive." (I doubt the expense would have been prohibitive for the wealthy hunters who supported the Cooperative Quail Investigation.)

"Such burning as proves desirable," wrote Stoddard (1931:412), "should preferably be carried on during the dampness of the night and against the wind if there is any blowing." Today we know that Stoddard wrote this anemic burning prescription under duress from the U.S. Forest Service and the American Forestry Association (Way 2006). These organizations were dogmatically opposed to burning for any purpose in the 1920s.

Tenant Farming and Primitive Agriculture

Stoddard's second great idea was dependent upon the emancipation of slaves in the South. This ushered in an era of tenant farming and associated small fields, lower successional patches intermixed with open pine (*Pinus* spp.) forests, and high landscape diversity. Bobwhites thrived under these conditions. Stoddard came to recognize that "early twentieth-century quail abundance—a big part of what made [the southeastern] landscape attractive to wealthy northerners seeking recreation in nature—was as much a cultural phenomenon as it was an environmental one" (Way 2006:507).

Stoddard's patchwork (also called primitive) agriculture meme has had great staying power. Today we know it is a sufficient but not a necessary condition for dense populations of bobwhites (Guthery et al. 2001). For example, in the mid-1800s Wisconsin bobwhites irrupted and achieved exceptional densities before agriculture arrived (Schorger 1946). Rangeland areas lacking any type of agriculture also can carry exceptional densities of bobwhites.

Defects in the Legacy

Any large body of information on any topic inevitably has strengths and weaknesses and *The Bobwhite Quail* is no exception. One error Stoddard committed was passing off as fact after-the-fact explanations of the cause of an event (this is called retroduction). For example, "many broomsedge [bluestem] fields are frequented by quail for nesting, roosting, and feeding that would by shunned by them but for the activities of hogs" (1931:355). This statement is plausible because of rooting and trailing by hogs (*Sus scrofa*). However, it is based on speculation and some other cause, such as some property of broomsedge fields that attracts both hogs and quail, might be the true cause. Or perhaps hogs are attracted to broomsedge fields to eat quail nests. Such cases of retroduction continue to inject false information in the guise of knowledge into wildlife science (Romesburg 1981).

A second boner he committed owed to the process of *invention*, or the confusing of plausibility and fact—retroduction on fantasy. "Weak chicks . . . normally are left behind very quickly by the brood, for the pace through the cover is regulated by the strong. . . ." (Stoddard 1931:197). That assertion certainly is plausible. However, its empirical confirmation involves seeing a brood (not easy), observing that one or more of its members are weak (how?), and following to document that the weaklings are left behind (not easy). How would you identify a weak chick versus one that simply got lost?

Here is another example of invention: "Although loss of developing chicks by drowning appears likely to be of little consequence in the rolling types of country, and is largely confined to the very young chicks lost in ditches, ravines, and gullies. . . ." (Stoddard 1931:202). The dependent clause beginning with 'although' certainly is plausible but whether it is empirically true was not known by Stoddard. The phrase containing 'is largely confined' is an assertion of fact that 'very young chicks' drowned in ditches and gullies. I would be surprised if Stoddard observed this because a collection of very young chicks that drowned (i.e., water in lungs) is quite implausible. Inventions such as this take on the aura of truth over the decades because they are birthed by an expert and frequently repeated. Humans have a tendency to soften skepticism when told statements are being made by experts (Freedman 2010).

Consider the following as a further example of invention: "If satisfactory sport and a safeguarded breeding stock are desired on the same ground year after year, the number of birds shot or otherwise harvested by man must be offset by control of natural enemies, improvement of coverts, or restocking" (Stoddard 1931:226). Stoddard is saying sustained yield harvest is impossible unless you reduce mortality or add to the standing crop. This notion may be rejected without recourse to experiment because predators have been taking a sustained yield of bobwhites for millennia. A quail dead of shotgun blast is no deader than one dead of talon. However, Stoddard's arguments are plausible, although wrong at the superficial level.

Lest you think I am unmercifully picking on Stoddard let me say that a lot of 'knowledge' about natural resources is based on invention. I have used (or committed) it myself. I provided information (Guthery 1986) on where supplemental water was needed based on annual rainfall. My arguments sounded good but they were based on nothing stronger than their melodious appeal to primitive logic.

Stoddard's book is and will remain a classic. Much of the natural history information, e.g., nesting, foods, movements, habitat requirements, and internal and external enemies, was sound for the times and valid today except insofar as times have changed.

Herbert L. Stoddard died with a copy of Aldo Leopold's *A Sand County Almanac* in his hands on 15 November 1968 (Gromme 1973).

ERRINGTON AND THE DOOMED SURPLUS

Convalescence and Creativity

Paul L. Errington's youth was characterized by debilitating illnesses and self-motivated, sometimes grueling, recoveries. An attack of polio in the summer of his eighth year led to prolonged incapacitation (Errington 1973). Likewise, he contracted rheumatic fever, an after effect of strep throat that may weaken heart valves, the last semester of his senior year in high school. This malady also resulted in a long recovery. Errington pressed himself physically with excursions in the outdoors to recover from these illnesses. Undoubtedly, these bouts provided him the opportunity to observe and participate in nature at nature's pace, and to mentally focus on same without having to commit much mind-time to the work-a-day world.

It is interesting that Aldo Leopold and Herbert L. Stoddard also had extended infirmities in their younger days. Leopold contracted Bright's disease (nephritis) in 1913 and remained incapacitated for 16.5 months (Meine 1988:131). Stoddard (1969:104) accidentally chopped his left leg with an ax and this wound and complications restricted his field activities from summer 1911 to summer 1912. These slow periods permit thoughts to foment and thereby foster the emergence of ideas because there is more time to think than during the conduct of normal activities. Convalescence seems to benefit creative thinking.

Errington was born 14 June 1902 on a farm near Bruce on the banks of the Big Sioux River in east-central South Dakota. Bruce had 272 residents in the 2000 census. The low human population, plus the nearby availability of farm, marsh, lake, and riverine habitat undoubtedly provided the young Errington with a cornucopia of wildlife and fish. Indeed, he was an avid hunter, trapper, and fisherman in his youth (Errington 1973).

The biographical information I have been able to retrieve on Errington makes little mention of his parents or family life. In his posthumous autobiography (*The Red Gods Call*) he mentions some activities of his mother and stepfather in a most general sense; names are not given. His stepfather, a proprietor of an ice cream parlor, gave the 11-year-old Errington a .22 rifle (Kohler 2011). His maternal grandparents (Johnson) had a farm on Lake Tetonkaha a short distance west of Bruce. Young Errington camped, fished, and hunted on the lake. His maternal uncle, Aaron Johnson, was a professor at the University of Wisconsin for awhile (Kohler 2011).

Wisconsin Studies

Early in his professional career, Errington became associated with Aldo Leopold and Herbert L. Stoddard. Stoddard and Leopold met in 1928 to select recipients of fellowships to conduct studies on important upland gamebirds in America (Stoddard 1969). The Sporting Arms and Ammunition Manufacturers Institute financially supported the fellowships. "A likely student for [a] fellowship, one with a favorable woodsman-trapper background, was available in the person of Paul Errington," Stoddard wrote (1969:220). Stoddard (1969:221) introduced Errington and Leopold to "key men and favorable terrain in the Prairie du Sac region," where Errington began research on bobwhites as part of graduate study at the University of Wisconsin, which he started in July 1929; the fellowship supported his work for 3 years (Errington 1948). He received his Ph.D. in 1932 and went to work for Iowa State University, where he remained for the balance of his career.

Compensation

Errington, in the general realm of ecology, probably is better known for his work with predator-prey relationships than for his great ideas regarding bobwhites, although these ideas overlap. Long before Errington the prevailing attitude on predators, for those who cared to have an attitude, was that predators kill and therefore take bounty from humankind. Errington (1967:225) took a deeper look:

> *In the case of Iowa muskrats [Ondatra zibethicus], the predation is centered upon overproduced young; upon the restless, the strangers, and those physically handicapped by injuries or weakness; upon animals evicted by droughts, floods, or social tensions; in general upon what is identifiable as the more biologically expendable parts of the population*.

Errington (1967:228) also recognized that life as a tangle of predators and prey, plants and sunlight, food webs and energy pyramids is replete with *compensation*. This tendency to compensate is "one of the prime upsetters of both theoretical and 'common sense' calculations as to how Nature's equations work."

Errington's recognition of compensatory mechanisms in nature was a stroke of genius. It involved (1) perceiving patterns hidden in complex relations, (2) dealing with the non-linearities that bedevil our as-the-crow-flies minds, and (3) having the fortitude to reject the so-called common knowledge of the tribe. These are intellectually deep and painful exercises that go somewhat contrary to human spirit. Perhaps they can be best explained by observing that in nature, what you see often is not what you get. The concepts will become clearer as I proceed through Errington's great ideas for quail.

Threshold of Security

The first great idea is that there exists a *Threshold of Security*, an imaginary construct that explains quail dynamics from fall to spring and provides a rationale for harvest management. Starting with his work at Prairie du Sac and continuing in Iowa, Errington observed a "rather constant year to year maximum" survival (Errington and Hamerstrom 1936:309). In other words, carrying capacity, "the *upper limit* of survival possible in a given covey territory as it exists under the most favorable conditions" (Errington and Hamerstrom 1936:308; emphasis in original) appeared constant through the years. Put in yet different words, barring weather emergencies such as blizzards, the number of breeders at the start of spring tended to constancy, at least in Errington's early results.

Errington (1945) called this number the Threshold of Security. Based on his field observations and data, when population abundance exceeded the threshold number, individuals were *vulnerable to* all forms of loss: egress (leaving the area), disease, predation, harvest, and other losses. Conversely, populations at or below the threshold were *resistant to* all forms of loss. Birds in excess of the threshold number were members of a *doomed surplus* (Errington and Hamerstrom 1936).

The threshold and doomed surplus concepts have direct relevance to harvest management: the shooting of a member of the doomed surplus has no effect on the population. The death of such an individual is fully compensatory—none lost from the breeding population for each bird bagged. Harvest, therefore, is inconsequential to bobwhite populations unless it involves taking birds from a population at or below the threshold level.

Inversity

I will show flaws in the threshold concept but first I discuss Errington's second great idea. It goes back to the compensation in nature that he recognized.

"Summer gains, as shown by numerical differences between spring and fall populations…, look highly variable; but … *they reveal certain patterns* (Errington 1945:13; emphasis added). "By the fall of 1932, it had been noted that summer gains tended to be in *inverse ratio* to spring densities…. For such years, we may ordinarily expect Prairie du Sac spring densities of 40 birds [this is really population size] to be followed by fall densities of about 140; spring densities of about 100, by fall densities of about 325; spring densities of 200, by fall densities of about 400; spring densities approaching 340, by fall densities approaching 440."

The above numbers show that as density of breeding birds goes up, productivity per pair goes down (inversity). Errington (1945:13) observed of spring pairs at Prairie du Sac, that 20 produced 5 young/pair in the fall, 50 produced >4 young/pair, 100 produced 2 young/pair, and 170 produced one-half young/pair. Errington observed that productivity as a function of spring density followed a reverse sigmoid curve. (I have accurately relayed what Errington reported, but I suspect he was reporting young/adult, not young/pair).

This Principle of Inversity is not only "one of the prime upsetters" (Errington 1967:228) of both theory and common sense but also a remarkable finding that holds approximately across wild vertebrates ranging from reptiles to mammals. Inversity is also called *density dependent productivity*. Density dependence is a mechanism which reduces the annual volatility of wildlife populations—a sort of population shock absorber that stimulates low populations and inhibits high populations. Errington discovered a truly great idea in the Principle of Inversity.

Contradiction

Just because the Threshold of Security and the Principle of Inversity are great ideas does not necessarily imply that they are without flaw. For example, the 2 concepts contradict each other. The threshold concept entails some constancy in breeding populations yet the inversity concept cannot be observed unless breeding populations are variable.

Regarding harvest management of bobwhites, the doomed or annual surplus model has been called into question. The model cannot possibly reflect nature in the case of variable thresholds (Romesburg 1981), which Errington (1945) posited. The additive model of harvest mortality (Roseberry and Klimstra 1984, Guthery 2002) seems to better explain the few empirical data available. However, for populations with low annual survival rates, the doomed surplus and additive models of harvest predict similar dynamics for bobwhites.

Scott (1963) considered Errington a deep thinker; I personally regard him as the deepest thinker of the Big Three. He took quailology beyond simple description and generalization into the realm of theoretical constructs (e.g., the Threshold of Security). Such concepts are key properties of elegant science (Guthery 2008).

Errington died in his sleep on 5 November 1962 (Schorger 1966) at the age of 60. One wonders whether his childhood bout of rheumatic fever might have hastened his death.

OTHER GREAT IDEAS

Leopold, Stoddard, and Errington are not the only biologists who have made important contributions to our understanding of bobwhites. Robert J. Robel and his students at Kansas State University have done superb work on foods and energetics. One particular paper, '*Bioenergetics of the bobwhite,*' (Case and Robel 1974), is a classic that explains a great deal about how bobwhites process calories and deal with ambient temperatures. Recourse to the information in this paper lays to rest many a phony notion about the thermal ecology of bobwhites.

John L. Roseberry and his students and colleagues at Southern Illinois University further developed the theory and practice of harvest management from the pristine speculations of Errington. '*Bobwhite population responses to exploitation: real and simulated'* (Roseberry 1979) is another classic. It is the type of paper so chock full of useful information that almost every sentence warrants highlighting. *Population Ecology of the Bobwhite* (Roseberry and Klimstra 1984) is a classic, underappreciated book.

Of course, in recent decades there have been a few hundred refereed articles on the management and biology of bobwhites, and research continues in the United States. This work is of variable importance. No doubt in time some of it will influence 'the vocabulary of everyone's thought' to the same extent as the work of Leopold, Stoddard, and Errington.

A final observation: a common property of the Big Three was extensive field observation coupled with analytical thinking on the mental information thus accrued. We appreciate them for observing *and* thinking. They rode to great heights on the back of natural history, without recourse to statistical folderol.

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