Letter will follow shortly.

This is the revised introduction.

Aldo Leopold

Errington

Ecological Society
Chicago 12/31/47

ROUND-TABLE DISCUSSION
Game and Fur Population Mechanisms

Introduction by Aldo Leopold

This discussion is intended to illustrate three facts, more or less new, in population research. It is confined to game birds and game and fur mammals, not out of lack of interest in other groups, but because time does not suffice to cover a wider bracket.

The three new facts are:

1. Species seem to shift in their population behavior patterns.

2. Reproduction and mortality are often best measured indirectly.

3. Sex and age composition promises to yield new clues to population mechanisms.

Shifts in Behavior

A decade ago we had our species neatly classified into cyclic and non-cyclic groups. Grouse, rabbits and hares, and some fur bearers were cyclic, others not. A few species exhibited irregular peaks called irruptions. These three types of behavior (cyclic, flat, and irruptive) came near being considered as species characters. What saved us from that error was the fact, even then visible, that grouse and rabbits were cyclic at high latitudes but not at lower ones.

Today these neat categories are all but shattered, and it is the animals themselves that did the shattering. I cite some cases which look like shifts in pattern.

The Pheasant Low. During the last three years the bottom has fallen out of this hitherto "flat" species. The decline was simultaneous in timing and almost transcontinental in scope. Even the fabulous Dakotas have felt the pinch. What are we dealing with?

Sportsmen say foxes. The decline did coincide in time with a transcontinental high in foxes, but the fox hypothesis is seemingly ruled out as a major cause by the fact that pheasants declined on foxless habitats heretofore supporting excellent stands of birds, such as Pelee Island in Lake Erie.

Some local researches ascribe the decline to agricultural changes, such as high-speed mowers (which are destructive to nests), or too much new plowing for grain. It appears to me that agricultural changes would produce a spotty abundance map, rather than a monotone of scarcity. Thus new plowing for grain would damage habitats which are short of cover, but improve others which are short of food.

The most reasonable hypothesis dealing with visible factors is bad nesting weather, but lethal weather would hardly hit with continental uniformity for

three years running. Moreover it would have to hit several times each year, for the pheasant is persistent in renesting.

The remaining possibilities are two: either the pheasant has become a cyclic bird and is sharing the present low of the ten-year cycle with the grouse, or else something drastic and fundamental has destroyed the recuperative capacity of the pheasant population.

A heavy population in western New York collapsed in 1936, in tune with the grouse, but has never recovered. This suggests that both of these conjectures may be true.

To sum up: the pheasant may be becoming cyclic in tune with grouse, but some lows persist and suggest either a skipped high or a permanent recession.

The Fox High. During the last three years an upsurge of foxes, nearly transcontinental in scope, has occurred in the northern states. Both species are involved in various mixtures, but reds predominate in most states. The peak population is now dying off, but in a spotty pattern. I say dying off because dead foxes were dug out of their dens, and sick ones were captured, at pupping time this spring, by a Wisconsin research worker.

Local upsurges of foxes have occurred before, but a transcontinental high is either new in the United States, or else failed to be detected. A red fox cycle of 10 year length is believed by some to have existed in Canada since 1900, but others do not construe the Canadian fluctuations as a cycle. The last two highs in the Canadian cycle (if there is one) have not coincided with the grouse cycle, but have lagged behind it as the lynx lags behind the hare. In Wisconsin grays dominated the high of 1935 and reds the high of 1944.

To sum up: a fox cycle common to the two species seems to be developing and moving southward.

Waterfowl Low. During the past two years a sudden drop has occurred in all ducks except those of the Pacific coast, and perhaps also in coot. The drop is especially severe in the black duck, which breeds in the Maritime Provinces where no drouth or botulism exists. Overshooting is the only visible cause for the decline in ducks, but there is no visible cause for the sudden decline in coot.

It seems premature to postulate a waterfowl cycle, but there is a bare possibility that one is developing; it seems no more improbable than a pheasant cycle would have seemed in 1942.

Prairie Grouse. One of the most baffling recent population behaviors is that of the prairie grouse (Pinnated and Sharptailed) in the Lake States. This is a zone of overlap between the two species. The main range of the sharptail lies to the northwest, where it is normally cyclic. The main range of the pinnate is to the south, where it is now too scarce to give a clear record.

Both species have been invading the cutovers of the Lake States, the sharptail moving eastward and the prairie chicken northward. Within this new range

both exhibit instances of collapse and recession similar to that already described for pheasants on new range in New York. In northern Wisconsin, both collapsed after a high ending in 1933. In the Upper Peninsula of Michigan the prairie chicken collapsed to the point of near-extinction after a high ending in 1941. In neither case could visible environmental factors have changed as rapidly or as uniformly as the birds did. Must we postulate a new "collapse" category characteristic of invaders?

Jacksnipe. In 1940 there was a collapse, evidently sudden, in the continental population of the Wilson's snipe or jacksnipe. A federal closed season for the ensuing 7 years has failed to bring more than a small degree of recovery. This bird was less heavily shot than the ducks, makes less use of the drouthy prairies for nesting, and as far as I know, is exempt from botulism.

Here then are four shifts in population behavior, which are difficult or impossible to explain in terms of known environmental factors. None of these changes were foreseen; management offers no remedies or controls other than rules-of-thumb.

One must conclude that we really know very little about population behavior, and that we are unable to manage wild animals until we know much more than we do now. Conservation then, as well as ecological science, demands a renewed effort to solve the problem of population mechanisms. This effort must dig deeper, must use more potent tools, and must expect to progress more slowly and patiently than any made in the past.

A New Approach to Populations

Such an effort is already under way, and this round-table is an attempt to describe and define it. I myself was not fully conscious of its newness until challenged to organize a presentation of it. I can see now that our failures of the 1930's have led gradually and almost imperceptibly to a radical revision of the fundamental techniques of wildlife population research.

Let me say at this point, before going any further, that the "new approach" is not really new; it is merely a new combination of ideas previously evolved in widely diverse fields.

The basic point of departure is the concept that a population is not merely a number, but an aggregate of sex and age classes in which the sex and age ratios portray, with mathematical accuracy, the current equilibrium of reproduction vs. mortality. Western cowmen used this concept to census their "invisible" herds of feral cattle. They computed, from a known tally of calves branded and steers shipped, not only a census but a mortality rate, and they knew, without finding all the carcasses, at what ages and in which sex the mortality occurred, and this in turn enabled causes of mortality to be deduced, and one habitat or range to be compared with another for productivity. Such computations had sufficient precision to enable bankers to loan cold cash for the purchase of herds which had never been seen in their entirety, and never would be.

The Forest Service later used this identical technique to compute the size of "invisible" herds, the owners of which were reluctant to pay full grazing fees. Many a court sustained or rejected suits which rested entirely on empirically

determined ratios between steer shipments (available in the freight office) and the herds which produced them.

Still later, when problems of excess deer and elk arose on the National Forests, the range managers in charge of both livestock and game quite naturally employed the same approach to the computation of censuses, the determination of sex and age compositions, and the computation of removals necessary to balance the herd with its available forage. I suppose these ideas migrated from big game to small game and fur field here discussed, but I offer this as a conjecture rather than as an assertion, for an idea cannot be banded like a pheasant, neither does it offer a bursa or a molt pattern for determining its age or previous condition of servitude. Ideas do not even conform to a taxonomy of species; like Topsy, they just grow up. So here is this one; let's see what it is good for, and how it differs from the older ideas which have failed to explain population behavior.

A Comparison of the Old and New Approach

The standard method in the past has been repeated censuses, plus special studies of factors suspected to be the cause of trouble. The limitations of this old method are best described, and the new method is best defined, by a direct comparison of the two.

If mortality in nests or young was suspected, we laboriously followed nests, candled eggs, counted broods, watched the menu of tethered hawks and owls, or learned the table-manners of egg-eating skunks. Such work was invaluable in identifying what decimators were at work, but the sum of all the deaths found never equalled the total which must have occurred. In short, the old method identified decimators, but failed to weigh them.

Today we measure the age-classes in the population resulting from the reproductive season and get a correct collective weight of all the decimators, with only one "if": movement. With banding, we can allow for that (or by using islands as study areas, eliminate it). We of course get no identification of the decimators; identification still depends on the old techniques.

One of the enigmas of a decade ago was: how many females reproduced at all? Today we examined egg-follicles or placental scars and read not only whether, but also roughly how much, reproduction occurred.

The central theme of the new approach is age-classes. It is a recurrent source of amazement to me to see how much can be deduced from a few years of aging of a sample population. In most cases censusing and banding are also necessary, but aging is the foundation of the new technique. Today aging includes not only the classification of the grown animals into old and young-of-the-year, but in gallinae the sub-classification of the young, by molt criteria, for date of birth. This yields a frequency curve which, when compared with the known breeding phenology, often reveals the vulnerable periods.

The speakers who follow will describe examples of the new approach to population questions.

Clues to Mechanisms

Even after the new approach has revealed how many individuals breed and die, and at what stage, there will remain the final and ultimate question of what they die of, and why. Our trouble heretofore has been that we lacked clues to narrow down the possible causes.

I will illustrate this by one example: cycles. In past years many possible causes, varying from sunspots to parasites, have been postulated. But does a "crashing" population really die, or is the crash merely its failure to reproduce? Age-classes will show what young survived in comparison with normal, and ovaries will show what females reproduced. With such clues, the remaining experimental tests to verify the nature of the cyclic mechanism will be vastly simplified.

The speakers who follow will now describe examples of the new approach to population problems, and the techniques which had to be worked out before the new approach could be tried. In order to reduce time, each speaker presents not only his own findings, but those of several others who have either published, or generously consented to the use of their data. Let me emphasize that this round-table presents not a finished piece of work, but a beginning. Our hope is that critical discussion here may strengthen the work still to be done.