September 21, 1944

Professor Aldo Leopold
424 University Farm Plan
Madison (5), Wisconsin

Dear Aldo:

I have thought over your comments of September 5 and will try to give my present reactions to them.

I am glad that you found the MS superior as a piece of writing, for it represents very nearly the best that I can do.

As concerns title and summary, I can't follow your reasoning at all. I think that both are exactly correct as they stand. In the matter of the title, I utterly fail to see how any coverage of the whole field of population phenomena is implied in the least. The title refers to contributions to a knowledge of population phenomena and contributions they may correctly be called. What the contributions are, the reader can see in the summary if he doesn't care to read the paper. The title is no more presumptious than any number of others one can bring to mind, including those in which Elton and his group refer to "population dynamics".

Without having the journal data at hand, I am under a tremendous disadvantage trying to appraise Kabat's exceptions to my figures (enclosures 1 and 2). In some cases, I think I can see, off hand, the reasons for the differences. Kabat's objection to my 31% non-emergency loss in 1936-37 seem due to my including loss in a covey that Gastrow said "might have been shot at". This leaves us stuck to some extent, for nobody can now determine how many, if any, quail actually were shot. Shooting at a covey, however, doesn't necessarily mean many birds killed -- an ordinary hunter being lucky to get one or two unless he succeeds in making a potshot -- so think my value of a 25-bird pre-emergency decline should not be far off. With this heavy pre-emergency decline, one would have expected the loss of perhaps as many more birds during the rest of the winter under nonemergency conditions, or a nonemergency survival close to the "100?" suggested in the table.

Lacking data at hand, I can't judge Kabat's figure of a non-emergency loss for 1937-38. If the nonemergency loss has indeed been as high as 30%, I would feel most surprised to have missed it. At any rate, it is clear that I pretty definitely decided that "the 1937-38 population lost only nine before the emergency period. . ." and made further reference to the "good survival of the majority of coveys up to midwinter". I wonder if the discrepancy might be due to differences in view as to what coveys were what, irrespective of the names by which Gastrow referred to them?

The situation in 1938-39 seems clear from page 22 of my MS, on which I say, "Even after making allowance for such departure [19 birds leaving the area], a mainly nonemergency loss of 22 is still fairly heavy . . ." The latter gave the "16%?" loss of the table. I felt that we would come closer to the truth by not considering the departed birds as lost, insofar as they were members of "two border coveys that otherwise lost only two birds" (hence had been reasonably secure), and probably stationed themselves nearby in habitat as good as they had left. When birds merely move a little off the area, I regard them for practical purposes as still present unless there are good reasons to the contrary.

Kabat's discussions of nonemergency losses for the winters of 1940-41 and 1941-42 disregard the all-important question of what losses or survivals could have been expected during totally mild and open winters. When this is lost sight of, losses actually occurring through emergencies in the early part or middle of a winter may be misleading, especially when the population is so insecure that nonemergency loss rates are high before, during, and after the periods of emergency. Considering the extreme vulnerability to predation of the populations for both winters and the inevitable intercompensations under such conditions, it is practically a certainty that the birds that died from midwinter emergencies (or their numerical equivalents) would have been eliminated anyway in the absence of the emergencies. This seems to me quite adequately explained on pages 23-24 of the MS. The distinctions thus made between midwinter and late winter emergency losses are of fundamental importance in dissociation of the variables.

On Kabat's page dealing with summer gains, his fall figure for 1936 differs from mine by five birds, the golf ground covey that was found on December 9 but not later. He thinks it highly probable that those birds belonged to other coveys in the neighborhood. I am sure that I must have considered such a possibility many times while having the data before me, but evidently concluded otherwise.

I have no way of explaining now the difference of five birds between Kabat's and my fall figures for 1937. He states, "The only possible way to get an approximation of the original figure of 163", etc., but knowing the many times that I worked over the data, I don't feel wholly convinced.

My guess is that I did include the last figures for the Greiber and E. Boehmer coveys in the spring total for 1937, probably on the grounds that this gave us a more nearly correct value for actual survival. I am not inclined to think that the fact that the coveys were not found on February 25 disproved their existance on the area, for the conditions for reading sign in 1936-37 were about the worst of the whole period of study. There also may have been some other evidence.

(I suspect that too much reliance on the names by which Gastrow designated coveys may have confused Kabat in places; my policy always has been to locate the covey as closely as possible and then judge for myself its identity in relation to habitat and other coveys. Gastrow's identifications were usually reliable but he occasionally made some obviously bad mistakes in referring to specific coveys during periods of massing, adjustment, etc.)

A possible explanation for my 1938 fall figure of 138 as distinguished from Kabat's 148 might be that for some reason I did not consider some birds as belonging to different coveys. If I really made an error in this respect, it has succeeded in persisting through a lot of calculations.

Much the same possible explanation may apply to the difference of 15 birds in 1940. If this truly is due to my failure to include the Pulvermacher covey, I would guess that there was evidence against this covey (or one of its neighbors) being a separate group.

At the risk of appearing stubborn, I may say that Kabat's versions have in no way caused me to doubt the essential correctness of my own summing of census figures and dissociation of emergency losses. It is perfectly plain that at least some of the differences are due to his failure to understand fundamental distinctions in method. Then, again, I worked over the data from "scratch" no less than, I think, four times since we started making serious efforts to prepare the Ms. It is true that I got some variations in those four reworkings but mainly pertaining to the early years. For one of these early years (I don't recall which one), I simply couldn't figure out how I got the total that I did, but decided to retain the published version on the theory that I should have known more about the detailed data at that time than I could hope to reconstruct a decade or so afterward.

Now to take up your questions as to precision of basic data:

The variations in dates of fall censuses always have been a headache. Ordinarily, the summing up was done for the earliest date on which anything approaching a view of the total population was possible. In the early years, this usually meant about the middle of December, and I simply referred to the census as of December; in later years, the times of first summing tended to come earlier, from the middle to the latter part of November, and, in comparative tabulations, I had all censuses as of November. For winters of low losses, such as 1929-30, this would seem to make little difference; but, for 1936-37, when the early season loss had such special analytical significance, a late initial census must be recognized as a real handicap. Heavier early-season loss in 1936-37, however, would only accentuate the trend shown.

As a rule, I disregarded the October census data in summing, unless there happened to some exceptional reason for using them.

I don't see your point about the earliness of the censuses for 1942-43 and 1943-44. I have only Gastrow's journal for the latter winter at hand, but few figures on coveys were obtained before November, and coveys seemed to be reported much as they were found, as in other years. The total fall census is given as for the first half of December.

Without minimizing the fact that variations occur, I think that you have overrated their possible influence on census figures, except for those for the winter of 1936-37.

My replies to Kabat's comments also pertain to subhead 2 on page 2 of your letter. Contrary to your expectation that the "percentage of surmise" is greater in the 1936-41 period, I have had, as already indicated, more trouble in tracing the origin of, and verifying, figures for some of the winters when I was on the area. In short, I am convinced that the "debatable margins" could be almost eliminated if we could get together over a table with the journals and a map. At any rate, in view of the fact that my final figures are the result of from four to a dozen or more separate reworkings, I would need to have pretty definite proof before losing confidence in them.

In (a) under your subhead 3, you wonder why I didn't project the pre-emergency loss rates of 1937-38 through post-emergency periods. Insofar as the most frequent experience of essentially secure coveys is to lose a few birds early in the winter and then suffer little or no loss later on, I can see no reason to apply the early season rate to the post-emergency period. To do this on a prorata basis would almost surely take us away from the truth. To use figures on actual decline after this type of emergency in computing nonemergency losses would also be risking much error, for, after a severe and general hunger crisis, one can never be sure how much of the predation, etc., isn't being borne by birds still suffering effects of the emergency. Everything considered, it would seem that under emergency-free conditions, the birds would have lost about what they did early in the season plus perhaps three or four later on; not being able to compute this more definitely, I put down "150?" in the table, which I would regard as wholly defendable and in keeping with the evidence presented in the MS.

The differences in method in estimating late winter nonemergency loss rates in 1936-37 and 1937-38 are due to differences in vulnerability apparent early in the seasons; they simply follow well-known facts.

I think that I already have replied to (b) of subhead 3. The emergency weather of 1940-41 and 1941-42 wasn't overlooked; it was appraised, on what I regard as the clearest of evidence, as being inconsequential in net effect.

Relative to the pheasants, Art Boehmer's summer releases in no way modify any conclusions given in the MS. The source of the birds, whether locally reared or artificially stocked in August, is immaterial; the pheasants were there in the fall, evidently having their effect on the fall levels of the bobwhite through their mere presence. Admittedly, Gastrow's early figures for pheasants have their questionable aspects, but they are all that we have and I included them for completeness. No implications are made that the summer gains are from spring-resident stocks of pheasants anymore than for the bobwhites; indeed, I think that the chances are against most of the pheasants present in fall having been raised on the area.

worked out by a professional mathematician whose competence in curve-

I don't know how much what I have said in this letter may influence you in the stands made in your discussion, but there are some points on which our views may or may not be basically divergent.

The evidence as to depression phases is in my opinion the real contribution of the MS and I think that the phase concept is well supported by data that I regard as of sufficient accuracy to permit reliance. In fact, despite haziness in spots and some possible error, the Prairie du Sac census data on wintering bobwhites are probably the most accurate ever obtained for any wild species on any large area over a long period of time. For sheer accuracy, they are probably inferior only to Mrs. Nice's data on the song sparrow; they far surpass all data of which I know that were gained through sampling techniques, trapping indices, etc.

The mathematical formulas are the descriptions of the sigmoid curves that come nearest to coinciding with the curves defined by the data points. Their detailed numeraäs and many decimal places do not imply perfection of the data; but they must be expressed this way in order to permit a mathematician to reproduce the designated curve on ~~a competance in curve~~ coordinate paper. Haymes fitting seems to be regarded as about the best on our campus. The fitted curves themselves do not coincide all the way with the data points (which explains differences in the stated errors of estimate); formulas can be worked out only for curves having certain mathematical properties.

From the formulas given may be determined essentially what rates of gain or nonemergency loss are to be expected at Prairie du Sac for just about any population density of bobwhites and pheasants during phases I and II so long as the trends apparent from the 15 years of data are maintained.

Let us here review the "debatable" margins between Kabat's and my figures. These relate to nine rates of gain or loss and to ten figures. In these, Kabat is definitely wrong so far as concerns nonemergency loss rates for 1940-41 and 1941-42. I doubt very much that he is right for the other three loss rates and feel that as much may also be said for his 1937 spring figure of 25 as against mine of 45. However, there seems to be more ground for question in the four fall density figures. If Kabat's fall versions were substituted for mine all the way through, only those for 1938 and 1940 would appreciably change the position of points on curves for phases I and II. For 1938, if Kabat is right, the rate of gain of bobwhites and pheasants would be 240%, which lies exactly in the phase I curve instead of the phase II. For 1940, Kabat's figure would give a gain of 119%, which would place it even better in the phase II curve than my figure does.

This boils down to a reasonably good possibility of one error big enough to influence conclusions as to phases, that for 1938, which is the least certain of the phase II years, anyway -- as is indicated in several places in the MS.

Your suggestion to include a section on possible errors would be more acceptable to me if I knew what to put in it. There seems to be continued disagreement between us as to what constitutes possible errors; I have already discussed in the MS the possible sources that I considered having a pertinent bearing upon the subject matter, with the exception of the recently recognized difference that Kabat's 1938 fall figure might make. Reference to the latter might simply be inserted in a suitable place. I am aware of no reluctance to point out a source of error or an assumption if I can see that there is one, but to obscure sound data by invalid qualifications seems to me to be doing the reader a disservice.

Your "clockwise" feature in the grouse data still doesn't look to me like any fundamental property, though I now see that it is more descriptive of the Cloquet population behavior than I had previously thought. Note, if you haven't, the nice counterclockwise progression of percentages of winter losses as plotted against density. But to emphasize this arrangement of the data only obscures in my opinion such significant things as thresholds, inverse ratios, and phase effects, which really govern populations. And neither Fisher's nor Edminster's data show much in the way of clockwise arrangement, even though they do show the typical "tightening" phases that seem characteristic of the classically cyclic species.

I shall try to correct anything in the MS that may unduly offend those who have studied cyclic phenomena through gross fluctuations. Nevertheless, my criticism is, I think, not only valid, but an extremely important one. The paper by Elton and Nicholson on muskrat cycles furnishes an illustration. They tied up muskrat declines with weather, and this cannot be challenged; but they made the mistake of assuming that these declines were the real cyclic declines and concluding thereby that the muskrat cycle preceded the main game cycle. If I paid attention only to gross fluctuations, I would conclude for the north-central muskrats much as Elton and Nicholson did. But when detailed population data are considered critically they show non-drought depressions of rates of increase, etc., in relation to muskrat density in 1936 and 1937, when a wide variety of higher vertebrates throughout the region, including grouse and hares, showed the same phenomena. This, I think, is proof, so far as it goes, of the real cycle in muskrats being synchronous with, rather than preceding, the general game cycle. The emergencies to which muskrats are so sensitive merely mess up the equation, in much the same way that undissociated winter emergencies do for bobwhite and hence lead to error as to what is cyclic and what is not.

I think that your criticism of the use of prairie chicken data is met by the qualifications made in the MS, especially by the quotation from Yeatter citing Davison.

Among your long-hand comments are a few that would seem to require replies.

Your 1937 paper is cited in the first of the two consecutive paragraphs giving wintering data for 1935-36 but not in the second, as I thought that the inference as to authority would be carried over. Now I doubt that this would be the case and shall add your citation number to the second paragraph as well.

I don't think that the origin of the Prairie du Sac pheasants, game-farm or otherwise, has any bearing upon the validity of the population figures. The plantings were plenty early in the season to permit natural adjustments much as would have taken place in the event of differences in hatch, movements, etc.

As concerns Fig. 10, the general alignment of the points is, as you imply, quite to be expected from the inverse ratios. No significant contribution in this respect is made by plotting the points. Its contribution lies in showing that the loss rates, even after making allowance for prorata and other shortcomings in computations, indeed do not occur in straight proportion to density. I don't see how we disagree on this. When we get a 49% rate of loss in 1936 from the same density that gives a 24% rate in 1943, we are not getting losses similarly proportional to density; and the loss rates for 1930, 1940, and 1941 are sufficiently far above the curve for the phase I years to emphasize this still more. I can't see anything wrong with the textual discussion. Later on, one of the main attributes of the low of the cycle is fairly well demonstrated to be loss rates more nearly in straight proportion to density than during "normal" times, when the rates may be greatly lowered in proportion to density by the operation of high thresholds, etc.

We probably still differ as to what constitute "fine-spun deductions". To my way of thinking the possible errors are too few and too small to affect the main conclusion arrived at: that different degrees of depression not only exist but also follow pretty definite patterns. I am not anxious to "stick out my neck" but to me the patterns are reasonably evident at this time from the P. du S. data and are strongly suggested by less complete data for other areas; to ignore them would seem to be as much of a mistake as never publishing research findings at all on the grounds that we never have the complete answers. In view of the conservativeness with which treatment is made, I don't see any more objection to introducing phase phenomena in this paper than to introducing thresholds and inverse ratios in previous papers. There is practically nothing in the way of speculation that isn't specifically labelled (and not very much of that) and the treatment says in effect that the 15 years of data from our main area and supporting data from elsewhere, so far as they go, would seem to warrant certain preliminary conclusions. Modifications of the original concept will doubtless be forthcoming, as they were for thresholds and inversity, but I regard it as nothing less than my scientific duty to lay what groundwork is currently in order -- especially since this may be my last major paper primarily dealing with the bobwhite. If I don't introduce phase phenomena (which seem to be of the most outstanding importance in population mechanics) to the best of my critical ability, who else will do it and when, and how well, if at all? I didn't clearly begin to see them myself until after 14 years of study of the bobwhite.

Considering my other increasingly demanding studies, this paper may represent the best contribution I may have in me on the particular subjects covered; and I had better give it "the works" now that I am doubtless as familiar with details as I ever will be.

As soon as the copy returns from the Fish and Wildlife Service, I expect to begin final revision, consulting again your comments as well as those of McAtee (who edited a copy as a personal favor) and others. I hope to get everything done by the end of the month, for the deadline for publication in January must be getting close.

I shall be most glad to get this out of my system. I don't feel more than ordinarily tired mentally but this thing has been so difficult to prepare and has complicated my schedule so much that I have had just about enough of it. I hope that in the course of time we will both feel the paper to be at least partly worth the grief it has cost us.

Sincerely yours,

Paul L. Errington
Research Associate Professor

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