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It is difficult to visualize convective dispersion, accounting for the short pulmonary gas transport times we measured; convective dispersion requires well-developed parabolic velocity profiles where the central streamlines move at twice the average velocity. Laminar profiles of this kind are unlikely to develop within the rapidly arborizing bronchial tree (gas molecules arriving at an average alveolus must traverse ≧ 20 generations of branches with a distance of only 3.5 diameters between bifurcations) (*1*). In this system of branching tubes, the faster-moving molecules in the center of one bronchus are divided at the branching point so that they tend to be moved into the slow-moving streamlines near the walls of the next branches, thus keeping convective dispersion to a minimum. Rapid radial diffusion in these narrow tubes further minimizes radial gas concentration gradients making significant convective dispersion even more improbable.

Because the bronchial tree is not open-ended, a tidal volume of 360 ml cannot be expected to reach the alveolar surface in a lung with a volume of 3600 ml by convective dispersion alone or, for that matter, by any other form of bulk flow. Indeed it can be shown by conservative calculations that diffusion is the primary mechanism of transport for the terminal 2 cm of the airways. According to Cumming *et al.* (*2*), still gas diffusion alone would require on the order of 1 second to transport detectable quantities of carbon monoxide over this distance; so even if we assume 0 time for bulk flow, still gas diffusion alone would require more time than we measure for the entire process. Obviously, diffusion must be facilitated in some way. In applying the Taylor analysis (*3, 4*) to the lung, radial diffusion reduces radial concentration gradients very rapidly. There does remain, however, a significant longitudinal concentration gradient which is the basis of our speculation concerning bulk flow-diffusion interaction. We agree, as we stated in our report, that the characteristic times must be compared for each branch in the bronchial tree before the question of transport mechanisms can be resolved. We also agree that the shape of the curve of carboxyhemoglobin formation requires further investigation.

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Statistics of Unseen Animals

Hanson (*1*) has proposed a new method for estimating the abundance of animal populations based on successive surveys. The ecologist is often confronted with the problem that the organisms are not all "seeable" or "catchable" by the methods available to him; this results in a sample which constitutes an unknown proportion of the total population. Hanson's procedure seems, in some remarkable way, to overcome this problem. Unfortunately, however, this conclusion is mistaken because of fundamental errors in the derivation.

It is proposed in Hanson's Eq. 4 that

$$y_1 = Y_1 (x_1/K)$$

where y_1 is the number of unseen animals occupying spaces in which one or more animals were actually seen, Y_1 is the total number of unseen animals, x_1 is the number of observed animals, and K is the population size. Since Y_1 is always less than K, this equation has the interesting but unrealistic property that y_1 is always estimated to be less than x_1.

Consider the case in which 1000 animals are present, on a grid of 100 spaces, with P, the probability that any given animal would be seen, equal to .10. One would expect, in a complete survey, to see approximately 100 animals and, since

$$Y_1 = K - x_1$$

or 900, Hanson's Eq. 4 would propose that there are 90 animals unseen on those grid spaces on which these 100 animals were seen. If we may assume, as Hanson suggests, that P is unaffected by distribution, then (i) if the animals are extremely patchy, say, all on one grid space, y_1 would in fact be 900 rather than 90; (ii) if the animals are randomly distributed, one should expect to see these 100 animals on a total of about 63 spaces (Poisson distribution), which would actually contain about 630 animals, of which 100 were seen; this would lead to an expected true value for y_1 of about 530 instead of 90; (iii) if the animals were evenly distributed, ten per space, one should expect to see the 100 animals on a total of about 65 spaces (binomial expansion), and y_1 would have a true value of about 550; and (iv) in the unlikely case that all 100 animals were seen one per space (biased observation methods), y_1 would be 900. Clearly, regardless of distribution, Eq. 4 gives extremely bad estimates of y_1 in this example; and, in fact, after much manipulation of such hypothetical cases, we are convinced that it is a very rare situation in which the estimates obtained are at all reasonable.

The quantity Y_1 (x_1/K) should, under Hanson's assumptions, be an unbiased estimator of the number of animals to be seen in a second, complete census, provided that the animals seen in the first census (x_1) were in some manner removed from further consideration. There appears to be no defensible logic, however, that would lead one to expect that this quantity will bear any consistent relationship to y_1, the parameter which it is purported to estimate; the above example indicates the kind of inconsistency to be encountered.

If Eq. 4 is inappropriate for estimating y_1, then Hanson's Eq. 5 is also in error, since it is derived from Eq. 4. In the four cases considered in the above example, Eq. 5 would lead to estimates of total population size of 100, about 250, about 250, and 100, respectively, rather than the known value of 1000. Since Eq. 5 is not an appropriate estimator for K, it follows that Hanson's Eq. 6 is also in error, that is, $(x_2/x_1)^{1/2}$ is not identical with $(1 - P)$, nor is it a reasonable estimator of that parameter.

Hanson's Eq. 7 purports to provide an estimator of y_1 when the distribution is even:

$$y_1 = Y_1(l_1/L_1)$$

where l_1 is the number of spaces on which animals were seen, and L_1 is the total number of spaces surveyed. This equation, however, also deserves more careful consideration. Based on Hanson's assumptions, the number of animals initially present on the l_1 spaces should be equal to $K(l_1/L_1)$, and y_1 would then be equal to $K(l_1/L_1) - x_1$. In view of Hanson's Eq. 3, y_1 can also be expressed as

$$\frac{Y_1}{K - x_1}[K(l_1/L_1) - x_1]$$

which simplifies to

$$y_1 = Y_1\left[\frac{l_1}{L_1} - \left(\frac{x_1}{K - x_1}\right)\left(\frac{L_1 - l_1}{L_1}\right)\right]$$

Under certain circumstances [for example, if $(l_1/L_1) \gg (x_1/K)$], it may be a good approximation to neglect the second term within the brackets and to set y_1 approximately equal to $Y_1(l_1/L_1)$; however, it is not an identity, as Hanson's Eq. 7 proposes, except in the trivial cases where either $x_1 = 0$, or $l_1 = L_1$.

If this (sometimes appropriate) approximation is treated as an identity, in the subsequent derivation of Eq. 8 estimates of population size become infinite. According to Hanson's Eq. 8,

$$\hat{K} = \frac{x_1^2\,(L_1 - l_1)}{x_1(L_1 - l_1) - x_2 L_1}$$

where x_2 is the number of animals seen on a second survey in which one searches for animals only on the spaces where no animals were seen in the first survey. On the basis of Hanson's assumption of an even distribution, however, x_2 can be estimated as $x_1[(L_1 - l_1)/L_1]$; when this value is substituted into Eq. 8, the denominator vanishes, and Eq. 8 becomes

$$\hat{K} = \frac{x_1^2(L_1 - l_1)}{0}$$

Since Hanson's Eqs. 9 and 10 are simply generalizations of his Eqs. 6 and 5, both of which are based on the erroneous Eq. 4, they also would appear to be of limited value. Hanson's equations do not permit the field ecologist to overcome the problem of "invisible" animals, since the method, if valid, would often be simpler in application than those methods previously available. It seems to us, however, that Hanson's observational technique is logically insufficient. The observed quantities, x_1, x_2, L_1, l_1, and l_2, do not uniquely determine the probability that an animal will be seen and cannot, therefore, permit reliable estimation of the actual population size without further information. Hence, the ecologist must rely either on improving his eyesight or on collecting that necessary additional information by more conventional indirect procedures.

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References and Notes

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Enright and Wormuth have shown correctly that my Eq. 8 (*1*) could not be valid (except in two trivial cases) when both the observed and unobserved animals were distributed uniformly. Although my solution implied that only the unseen animals were evenly spaced, in nature the seen animals would seldom be clumped while the unseen ones were distributed uniformly. It seems intuitively that the general approach of Eqs. 7 and 8 could perhaps be modified to cover more general situations, but I have no suggestion on how to do it.

Enright and Wormuth claim that my main model, Eq. 10, has "limited value" because it is "based on the erroneous Eq. 4." However, they attempt to show that Eq. 4 is erroneous by using a hypothetical example involving four distributions of the animals, each of which would be highly unusual among real populations. In addition, they select the value of P as .1; on this basis q (where $q = 1 - P$) has a high value of 0.9, whereas I recommended that the sampling be designed to make q equal to 0.7 or less. Animals are usually distributed contagiously (a clumped distribution). Therefore, surveys made on reasonably small spaces would not yield a random distribution as in case (ii) of Enright and Wormuth or an even distribution as in their case (iii). Certainly all of the population would not occur on one sample space as in their case (i) nor would clumped animals be observed at the rate of one per space as in their case (iv); and if the worker did encounter such rare events he would surely do further sampling.

Enright and Wormuth say that y_1 has the "interesting but unrealistic property" that estimates of y_1 will always be less than those of x_1. To me this is not necessarily unrealistic, and, even where it is, the combining of results from several surveys may tend to give average estimates of y_i that are closer to the calculated value of y_1. In the places where the observer sees some animals, visibility is probably better, on the average, than elsewhere, thus leaving fewer unseen animals on such plots than could otherwise be expected. Also, most of us may subconsciously tend to look a little harder for additional animals after some have been sighted on a sample plot. Both factors will tend to lower a potential overestimate of y_1. And in the numerous cases where q is smaller than P, or only slightly larger, y_1 should certainly be smaller than x_1.

In Eq. 10, the main equation of my report (*1*), I have given a weighted average to the results of several surveys in an attempt to estimate the average value of P_i, since the actual probability of seeing the animals during successive surveys tends to fall lower and lower. If the various estimated removals of unseen animals are at first less than their actual removals, then the falling P_i's should in the later surveys cause the reverse tendency, thus giving some compensation when surveys are summed.

In my report (*1*) I gave the results of a few experiments with Eq. 10, and here I give the results from another experiment on laboratory mealworms (*Tenebrio molitor*). Eight students each had a small colony of mealworms and each student, as part of a class project, made five quick, cursory counts of his mealworms by the methods previously described. The number of animals seen in the eight colonies as a whole during each successive survey were: X_1, 270; X_2, 99; X_3, 44; X_4, 42; and X_5, 24. As the samples were summed cumulatively and substituted in Eq. 10, the following estimates of the total population were obtained in succession: 685, 714, 816, and 839. The total number of animals actually present was 848.

My Eq. 10 may possibly turn out to have "limited value" but in my opinion Enright and Wormuth have not yet demonstrated this theoretically nor experimentally. In their view evidently, the final estimate of 839 mealworms should rarely have been so close to the actual population size of 848.

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