Varley[2], in discussing Nicholson's equation :

$$N_E = \frac{g - lg - wg}{q}$$

gives the following definition of terms, to which I have ascribed dimensions, using M, L and T in their usual sense.

N_E = equilibrium population density : L^{-2} for terrestrial animals

g = food supply : if this is presumed to mean 'on unit area', $ML^{-2}T^{-1}$

l = fraction of food lost to extraneous factors : (numeric)

w = fraction of food wasted by surplus individuals that fail to mature : (numeric)

q = quantity of food required to complete development : M

This makes the equation balance, but also makes it almost useless in practice since only in very special circumstances, such as the development of an egg, do situations occur in Nature in which there is a discrete food supply that is not added to during the life of the population.

Nicholson[3] gives the same definition of N_E, and effectively the same of q, but defines g as the rate of generation of the governing requisite, and l and w as fractions of this. In the case argued by Varley, where the governing requisite is food, the dimensions of the equation then become :

$$[L^{-2}] = [ML^{-2}T^{-1}]/[M] = [L^{-2}T^{-1}]$$

which is absurd. There is confusion between the rate of supply of food and the total quantity required. (Both may be important to the animal, since it needs not only enough food but also enough at the right time.)

When one turns to Nicholson's original paper[4], one finds the same definitions for N_E, g, l and w, but q is said to be the maintenance quantum in the procurement field (i) of an individual, so that :

$$G_E = q/i$$

where G_E is the equilibrium density of the governing requisite. This would seem to make the dimensions of q to be M, as before, so that the equation still does not balance. It is difficult to see how equations that fail to pass the most elementary kind of dimensional check can be of any help in the study of ecology.

I have had the benefit of discussing the method of dimensions with Mr. G. R. Noakes.

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[1] Focken, C. M., "Dimensional Methods and their Applications" (London, Edward Arnold & Co., 1953).
[2] Varley, G. C., *Nature*, **183**, 911 (1959).
[3] Nicholson, A. J., *Nature*, **183**, 911 (1959).
[4] Nicholson, A. J., *Aust. J. Zool.*, **2**, 1 (1954).

MILNE gives his case away at two points in his argument. His first difficulty is largely semantic. He prefers the term 'maximum density' where Nicholson used 'equilibrium density'. In population experiments begun at low densities, where the numbers rise asymptotically to a maximum, both terms are equally applicable. However, populations often overshoot the equilibrium denstity and settle down to this value afterwards ; or they may be begun experimentally at levels above the equilibrium. Nicholson's more general term is applicable to all these cases, whereas Milne's is not.

Nicholson's experiments have shown how equilibrium population densities vary with the conditions, and surely all would agree with Milne that this relationship is one of cause and effect. This in no way renders Nicholson's terms balance or equilibrium less suitable.

In his last paragraph Milne fails to see that my general statement that w must be treated as a variable which is a function of the population density N does not conflict with the more specific relationship which he proposes—especially as his N' must itself be a function of N. Although it is critical to the understanding of the behaviour of crowded populations, the actual form of the relationship remains undiscovered. Finally, if Nicholson's formula is, as Milne claims, an elaboration of one already used by farmers, it seems perverse to suggest that it is useless to those ecologists studying single species cultures.

Yapp's communication raises the important question of the dimensions to be attached to the terms in Nicholson's equation and I am very glad to have the opportunity of clarifying the matter. Nicholson (*l.c.*, p. 30) says that the maintenance quantum q represents 'an average of the varied amounts of the given requisite obtained by different individuals *in unit time* ehen living under equilibrium conditions ' (my italics). Andrewartha in *Nature* of January 17 incorrectly redefined q as 'the amount [of the requisite] required by one individual to complete its life cycle', and I regret that in our replies in *Nature* of March 28 both Nicholson and I used similar definitions and wrongly omitted the vital words "in unit time '. Nicholson's unfortunate choice of the terms "maintenance quantum ' and ' procurement field ' for what are (as Milne correctly says) rates of feeding and of searching is, I consider, partly to blame for the loose way in which the terms have been discussed.

Since the dimensions of q, g and i all include T^{-1} Yapp's difficulty disappears. The time unit might, as Milne suggests, be taken as the time for an average individual to develop to maturity, but must in any event be the same for each of the terms.

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Cause of Wear in Sheeps' Teeth

IN New Zealand the problem of wear in sheep's teeth is acute on some pastures, and as a result of detailed investigations, Barnicoat[1] suggested that wear is due to the abrasive action of the fibre in herbage although he could not correlate the amount of fibre in herbage with the extent of wear. While Barnicoat (p. 586) found no evidence to justify further studies on the mineral content of herbage we, on the other hand, believe that such studies may provide the clue that leads to an understanding of wear.

Our approach is based on the knowledge that opal-phytoliths are secreted within pasture and fodder plants in varying amounts. In fact, practically all the silicon in mature plants is in the form of these solid mineral particles[2]. Furthermore, we have obtained opal-phytoliths in the fæces of sheep and find many of them to be in a fractured condition. The fact that opal is a relatively hard mineral leads to the idea that opal-phytoliths in pasture and fodder plants are largely responsible for wear in sheep's teeth.

We have carried out relative hardness tests by two methods on the molars and incisors of the sheep and on opal. The teeth examined were from a four-year-old sheep which had been fed on pasture. They showed considerable cratering of all molars and rather less

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