Letters

Modelling transmission: mass action and beyond

In a recent review in *TREE* [1], McCallum *et al.* say that they are confused by the terminology related to mass action in disease transmission that we introduced in Ref. [2]. In retrospect, we see that our description of the expression 'βSI' (where S is the number of susceptible hosts, I is the number of infected hosts and β is the transmission coefficient) using the words 'pseudo mass-action' (thus implying that the description is not a correct rendering of mass action) might be confusing when one does not restrict this, as we did, to a case where S and I are numbers.

The relationship between the intensity of contacts between individuals on the one hand and population size on the other, is a complicated issue that deserves more attention and a reviewing progress, as in Ref. [1], is therefore to be applauded. Several fundamental problems with density were, however, neglected, particularly the question of how to define 'density' for a natural population. Behavioural patterns, as well as heterogeneity of the environment, create nonhomogeneous distributions of individuals that are not accurately characterized by simply dividing the number of animals by the total habitable area. In populations that are fluctuating in size, one is also faced with the question of how changes in numbers are related to changes in density (i.e. does population growth come with an increase in area?).

Previously [2,3], we discussed two points related to modelling transmission and we take this opportunity to explain them again in a different way:

(1) Often in transmission models, host populations are compared that differ in number, but not in spatial density of animals [3–5]. Moreover, variations in number but not in density also occur for farmed animals where the same housing system in farms of different size will lead to different numbers of animals that are, however, kept at the same density. In more natural situations, density might be determined by animal behaviour that is independent of area size [6].

(2) Modelling density dependence could be considered a logical next step in modelling transmission. However, density is neither easily defined nor easily measured. McCallum *et al.* [1] discuss density dependence as though these problems do not exist. Can transmission ever be modelled as depending on numbers-per-unit-area in a reliable way? Ignoring the discussion on how density is measured and introducing *ad hoc* (i.e. not mechanistically derived) transmission functions based on density does not necessarily help us to better understand transmission. One mechanistic argument discussed by McCallum *et al.*, the Holling type argument, was first introduced into an epidemic context by Dietz [7], and shown to be problematic in this same context by Heesterbeek and Metz [8] (quoted in Ref. [1] for another reason).

The key issue is how to model the number of contacts with other individuals per unit of time per individual. Instead of modifying the transmission function, it could be worthwhile to look at other ways in which contact structures can be incorporated in models. For example, for farmed animals, the whole study population can be viewed as a metapopulation of groups of animals, where within-group transmission is modelled best by mass action and between-group transmission by explicit use of connection matrices [9]. See also Ref. [10] for elaborations on several of the issues raised here.

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Response from McCallum, Barlow and Hone

In our recent article in *TREE* [1], we were very careful to say that De Jong *et al.* [2] had been 'widely interpreted as claiming that βSI did not represent "true mass action"'. It is the way in which their paper has been interpreted, rather than the paper itself, that is the problem. Their paper is restricted to situations in which host population size changes, but density remains constant and, in that special case, βSI (where S is the number of susceptible hosts, I is the number of infected hosts and β is the transmission coefficient) is indeed not a correct representation of the mass action assumption. The problem has been that this is a special case, one that we think is quite unusual in free-ranging animal populations, although it can be generated experimentally, and can occur in farmed animals. As we noted [1], seal colonies are one of the few natural situations where it is likely that transmission is better modelled with population numbers rather than densities per unit area, and this is the example [3] of a wild population referred to in De Jong *et al.*'s [2] response to our paper. In almost all other natural populations, an increase in host population size will lead to