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Non-IFD movements: reflections on past work and prospects for future developments

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The paper by Don Hugie and Tamara Grand (2003) confirms the validity of their previous results that had been called into question by us. This new paper reassures us that both parties are still of one mind regarding what we feel is the key message from the original paper of Hugie and Grand (1998): that non-IFD movements are likely to be crucial to our understanding of animal distributions.

The new results presented by Don and Tamara bear strong similarities to those presented previously in both Hugie and Grand (1998) and Ruxton and Humphries (1999). Using an analytic model, Hugie and Grand (1998) predicted a 'single stable distribution' for each competitor type, while Ruxton and Humphries' (admittedly crude) individual-based simulation model predicted a distribution of potential equilibria resulting from shifts from one equilibrium to another over time. Don and Tamara now show that, when their original model is translated more carefully into an individual-based simulation, 'variation in the competitor distribution appears to be centred on the equilibrium distribution of the large population scenario' (Hugie and Grand, 2003: 141). Thus, although a dynamic equilibrium results in the large population model, when a finite population is considered, 'the probabilistic nature of competitor movements causes the flow of individuals moving in either direction to vary, preventing any competitor distribution from persisting indefinitely' (p. 141). The main difference from our results is that we predicted temporal variation with the system moving between a number of possible IFD distributions, whereas Hugie and Grand (2003) predict similar variation centred on a single distribution. Hugie and Grand's (1998) analytic treatment of an infinite population size does not predict temporal variation at all.

It is worth remembering that while Don and Tamara did find errors in our original computer code, they also show that, after removing these errors, 'the basic results of Ruxton and Humphries remain the same' (Hugie and Grand, 2003: 144). However, we certainly do not wish our programming mistakes to detract from our original conclusion that Hugie and Grand (1998) produced an important and interesting result that merits further work to

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explore its generality. We also believe that to do justice to non-IFD movements requires an explanation of why a single dynamic equilibrium occurs in the model presented in 2003 by Hugie and Grand. To allow further exploration of these results, we need modelling that is explicit and precise in its definitions and implementation of assumptions. Furthermore, these assumptions should be defensible in terms of our understanding of ecology. Don and Tamara have demonstrated that our previous work did not score as highly as we would have liked on these criteria. On reflection, it is clear that scoring highly on these criteria is actually quite challenging, as we discuss below.

One of the key messages of Don and Tamara's new paper is that the behaviour of the system is sensitive to the relative frequency of non-IFD to IFD movements. Although they suggest that the relative strength of non-IFD movements will often be weak (Hugie and Grand, 1998, 2003), we remain to be convinced. We are convinced, however, that there is a strong need for IFD theory to move forward, and to do this we must have empirical data on non-IFD movements. Indeed, we must now seek to generalize these results to different distributions of phenotypes and different ways of describing competition (e.g. Humphries *et al.*, 1999, 2001; Ruxton, 1999). As in their previous paper, Hugie and Grand's new results lead to the prediction of slight 'under-matching'. This outcome is comforting, as it agrees with what is commonly seen in tests of the IFD (Kennedy and Gray, 1993). However, this result may be sensitive to perturbations to the very simple rule for non-IFD movements used in the current model. It would, therefore, be helpful if there were empirical studies of not just the frequency of non-IFD movements, but also of the mechanisms that drive them, since ultimately we will want to predict levels of non-IFD movements in different ecological circumstances.

We further agree with Don and Tamara that population size matters. When population sizes are small, analytic approaches cannot address movements of individual animals and the deviations from a steady state that these movements produce. Here again is a challenge to theoreticians: to resolve how large a population has to be before it can be modelled deterministically. This point has been dealt with conclusively in the study of childhood diseases, where even populations of one million individuals still require individual-based simulations rather than deterministic ordinary differential equation approaches (Grenfell, 1992). Crucially, Hugie and Grand's (2003) results show that, 'except for extremely small populations, such as those typical of aquarium studies, the competitor distribution will continue to resemble an equal competitors IFD' (p. 133). Our point now, as previously, is that, at the scale of laboratory experiments, temporal variation in the distributions attained is a key part of the system. We originally simulated 72 individuals, 'since most experimental tests use fewer (normally considerably fewer) than 100 individuals' (Ruxton and Humphries, 1999: 635). Similarly, Don and Tamara suggest that 72 is a size representative of most laboratory studies and describe this as a small population in ecological terms. Given that variation in competitor distribution in their model decreases to a point where the competitor distribution rarely deviates outside the magic zone for populations of 720 individuals or more, they suggest that their 1998 conclusions are appropriate for all but the smallest ecological populations. We suggest that most ecologically relevant interactions occur at much lower numbers than that of the whole population (or a significant proportion of it). This difference in choice of appropriate population size needs to be resolved by theoreticians – we have to decide whether our models can be tested with dozens of fish in controlled laboratory conditions or whether we need field systems of thousands of individuals to test the theory. Studies of ideal free distributions have repeatedly shown that

the latter approach is not ideally suited to elucidating mechanisms or allowing individuals to be monitored (Tregenza, 1995).

If we are dealing with the behaviour of interacting individuals, then the timing of events matters (Huberman and Glance, 1993; Ruxton and Saravia, 1998; Schönfisch and de Roos, 1999). Don and Tamara rightly question the ecological relevance of our method of event timing. However, one of the reasons that we adopted the method we did was to avoid large numbers of individuals simultaneously changing patch. While Don and Tamara do allow simultaneous movements, this has the drawback that, if the probability that a competitor switches between habitats during a given time period is too large, some proportion of the population will oscillate back and forth between habitats. As they point out, 'a large proportion of the population may move from one habitat to another for IFD reasons, only to find the payoff in the new habitat sufficiently depressed to cause them all to return to their original habitat in the very next time period. Such oscillations can continue indefinitely' (Hugie and Grand, 2002: 151). Don and Tamara cope with this artifact by introducing an *ad-hoc* dampening factor. Neither approach is wholly satisfactory, and the most pressing need for further work in this area is the development of clear methodology for coping efficiently with the relative timing of events.

In summary, the results provided in Don and Tamara's paper greatly strengthen our belief that their focus on non-IFD movement is a valid and important contribution to our understanding of natural distributions of individuals. We are relieved that there is no substantial unresolved dispute between ourselves and Don and Tamara. Finally, we hope that the discussions in these two papers serve as a reminder about the care that must be taken in formulating simulation models; it has certainly been useful to us.

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