The distribution and abundance of mammals: density dependence in time and space

Douglas W. Morris, Centre for Northern Studies, Dept of Biology, and Faculty of Forestry, Lakehead Univ., Thunder Bay, Ontario, Canada P7B 5E1 and Per Lundberg, Dept of Animal Ecology, Swedish Univ. of Agricultural Sciences, S-901 83 Umeå, Sweden (present address: Dept of Theoretical Ecology, Lund Univ., Ecology Building, S-223 62 Lund, Sweden)

Ecologists have known, at least for the 40 years since Andrewartha and Birch published their influential and enduring *Distribution and abundance of animals*, that population dynamics are influenced by events in both time and in space. Source-sink dynamics were highlighted 20 years ago (Lidicker 1975), and had been suspected by Joseph Grinnell (Grinnell 1943, MacArthur 1972). There is, nevertheless, no coherent theory that integrates spatial and temporal dynamics, and no widely acknowledged set of protocols to evaluate their joint and interactive effects.

There are, of course, good reasons why the theory and protocols are not in place, and why the unfortunate legacy of polarized debates on regulation continues (Murray 1994). Interactions in density dependence in time and space, many of which are likely non-linear, complicate population dynamics. But complications in sorting out interactions among processes of population regulation in time and in space in no way detract from the other reality that populations, and the machinery that manipulates them, are themselves dynamic in space and in time. It makes no sense to assume otherwise.

It similarly makes no sense to assume that the whole is so complicated that it is likely to be mimicked only by interactive forecasting models constantly updated with field data. Our goal, for the vast majority of species that cohabit the planet with us, must be not to simply forecast the future, but rather be an understanding of the interactions between spatial processes on one hand, and temporal changes in population dynamics on the other. The hope is that we will discover the new insights into population regulation that can guide our research as we head toward the 50th anniversary of Andrewartha and Birch's book.

In July 1993, the Sixth International Theriological Congress was held in Sydney Australia. It seemed appropriate that we commemorate the contributions of Andrewartha, Birch, and others in the Australia tradition, with a symposium dedicated to furthering our understanding of population regulation. We wanted the symposium to be more than a review of past studies, or even of our current knowledge of population regulation. We wanted it to represent, as well, a new beginning in our attempts to understand distribution and abundance. We invited a small group of ecologists with provocative ideas on density dependence to join us. We challenged our speakers to develop and to test new ideas on how populations of mammals may, or may not, be regulated in both time and space.

The papers that follow are the product of that challenge. The first, by Sinclair and Pech, establishes the groundwork for the meaning and interpretation of density dependence. We hope that it will finally end the polemics on whether density dependence occurs or not, and point us toward more productive avenues of research that evaluate creative ways of looking at density dependence, and its ecological and evolutionary implications.

Åström et al. introduce new models that incorporate sequential density-dependent processes. Different sequences yield dramatically different population dynamics and may account for many regional differences in population regulation. It is intriguing to speculate on the role that sequential density dependence may play in the evolution of life histories that, in turn, modify the nature of density dependence.

The evolutionary theme is explored by the next two papers. Holt evaluates the importance of dispersal between source and sink habitats on the evolutionary dynamics of niches. One of the questions he answers is, under what conditions are sink habitats evolutionarily stable? With passive dispersal, the more severe sinks become, the more likely it is that source-sink dynamics will be stable, and paradoxically, the greater the risk of extinction. As Holt notes, "those populations most in need of evolutionarily responding in their niches are the very ones least likely to do so". Another paradoxical result, given the history of work on source-sink regulation, is that populations whose density-dependent dispersal is driven by interference are the ones most unlikely to demonstrate stable source-sink dynamics.

Joel Brown expands the study of density-dependent dispersal and habitat selection to three habitats. The results reveal a sobering array of possible forms of adaptation and community organization. The number of evolutionarily stable communities expands exponentially with the number of habitats. Certain combinations of evolutionary strategies and their resulting communities are more likely than others. The stability of ecological communities will thus vary from place to place, and through time. No wonder that ecologists have argued so long about organizing forces in ecological communities. Brown's work is a poignant reminder that we must link our interpretations of communities to the evolutionary and co-evolutionary strategies of their members.

The final paper by Morris attempts to put the theories into practice with a joint analysis of temporal and spatial density dependence. It uses long-term data on the density and fitness of white-footed mice living in adjacent habitats to search for tell-tale interactions between fitness, density, season and habitat that confirm Holt and Brown's emphasis on density-dependent habitat selection. Complex seasonal interactions are reminiscent of Åström et al.'s models on sequential density dependence. Perhaps we do possess the basis of theories, tools and protocols necessary to understand interactions between time and space that characterize the dynamics of real populations.

The symposium would have been impossible without the assistance of the organizers of the Sydney Congress, most especially Barry Fox and Michael Augee. We are also indebted to the many referees whose detailed reviews helped us prepare the symposium for publication. We thank the editorial board of Oikos for supporting our publication efforts and for publishing the papers together in a single issue. Most importantly, we thank our guest contributors for their many novel ideas on density dependence and for their patience and understanding as we moved, slowly at times, toward publication.

This collection of papers is dedicated to Graeme Caughley.

References

Grinnell, J. 1943. Joseph Grinnell's philosophy of nature. – Univ. California Press, Berkeley, CA.

Lidicker, W. Z. Jr. 1975. The role of dispersal in the demography of small mammals. – In: Golley, F. G., Petrusewicz, K. and Ryzkowski, L. (eds), Small mammals: their productivity and population dynamics. Cambridge Univ. Press, Cambridge, pp. 103–128.

MacArthur, R. H. 1972. Geographical ecology. – Harper and Row, New York.

Murray, B. G. Jr. 1994. On density dependence. – Oikos 69: 520–523.