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Meeting report

Lost in space? Searching for directions in the spatial modelling of individuals, populations and species ranges

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The workshop ‘Spatial models in animal ecology, management and conservation’ held at Silwood Park (UK), 9–11 March 2010, aimed to synthesize recent progress in modelling the spatial dynamics of individuals, populations and species ranges and to provide directions for research. It brought together marine and terrestrial researchers working on spatial models at different levels of organization, using empirical as well as theory-driven approaches. Different approaches, temporal and spatial scales, and practical constraints predominate at different levels of organization and in different environments. However, there are theoretical concepts and specific methods that can fruitfully be transferred across levels and systems, including: habitat suitability characterization, movement rules, and ways of estimating uncertainty.

Keywords: spatial modelling; dispersal; movement; population dynamics; biogeography

1. INTRODUCTION

The spatial dynamics of individuals, populations and species ranges are of fundamental interest to ecology and evolution. Spatial behaviour is also of great relevance to conservation practice (Araújo 2009).

Spatial protection measures have long been a cornerstone of terrestrial conservation and, as the same approach is now being extended to the marine environment (Lorenzen *et al.* 2010), an opportunity arises to review modelling tools that could inform spatial management.

The workshop ‘Spatial models in animal ecology, management and conservation’ hosted by the NERC Centre for Population Biology at Silwood Park (9–11 March 2010) aimed to synthesize recent progress in the spatial dynamics of individuals, populations and species ranges; to search for connections between level and approaches; and to provide directions for research. Marine and terrestrial biologists presented current research on animal movements, distributions and spatio-temporal dynamics. Integrating presentations with modelling exercises and group discussions, the workshop provided rich opportunities for making connections and identifying new directions. In this report, we synthesize our understanding of the relationship between animal movement and spatially explicit population dynamics across terrestrial and marine environments in three steps: (i) reviewing modelling approaches used at different levels of organization, (ii) identifying key approaches for connecting levels and integrating empirical and theoretical approaches, and (iii) distilling directions for research.

2. MODELLING SPATIAL DYNAMICS OF INDIVIDUALS, POPULATIONS AND SPECIES RANGES

Modelling at all levels of organization can be carried out using empirical or theory-driven approaches. Presentations at the workshop included examples of both approaches, at all levels.

(a) *Individuals*

Much research at the individual level is focused on modelling short-term movement behaviour and the emergence of home ranges. This is often done using empirical, random walk models but a more theoretical basis for such analyses is emerging (Nathan *et al.* 2008).

Detailed individual movement observations are available for terrestrial vertebrates and it is in this context that movement models are most advanced. Börger (University of Guelph, Canada) presented an approach for modelling dispersal in order to understand population redistribution and quantify long-term survival consequences for reintroduced elk (*Cervus elaphus*) using nonlinear mixed effects models. Bunnefeld (Swedish University of Agricultural Sciences, Sweden) extended this approach to a seasonal migration model consisting of two stationary phases (summer and winter) and two diffusive phases (spring and autumn migration). Using nonlinear mixed effects models fitted to displacement data allowed him to separate migratory from non-migratory individuals and to quantify individual- and population-level variation in migration of Scandinavian moose (*Alces alces*).

Linking space use and movement to habitat is an important step towards more mechanistic modelling, and of crucial importance to many conservation problems. A key question is to what extent habitat suitability inferred from observed density distributions

is transferable in space and time. Matthiopoulos (University of St Andrews, UK) proposed a new way of addressing this problem: generalized functional response (GFR). The GFR can be used to model changes in resource-driven space use as a result of changes in habitat availability, using them to predict population distributions in unobserved environmental scenarios. He illustrated this approach using telemetry data on space-use from 11 wolf (*Canis lupus*) home ranges. Börger discussed links between habitat distribution, population size and variation in mating success for European roe deer (*Capreolus capreolus*) by modelling the dynamics of home range size. Memory of the distribution of food resources is generally considered an important mechanism driving animal movements. Van Moorter (Norwegian University of Science and Technology, Norway) presented a random walk model in a dynamic landscape with patch depletion and renewal which gives rise to home range emergence (Van Moorter *et al.* 2009). Temporal changes in attractiveness of previously visited patches, following the landscape dynamics, leads to systematic return to these patches and, in the long term, to the establishment of a stable home range.

Singh (Imperial College, UK) showed through time-series analysis of distribution and movement patterns that the natural migratory movement of Saiga antelopes (*Saiga tatarica*) can be severely influenced by anthropogenic factors and, that in avoiding areas of high disturbance, migratory species might be pushed into less suitable habitat.

In comparison to terrestrial systems, movement studies of animals in marine systems are hampered by infrequent and inaccurate locations, and often lack of concomitant habitat information. This has led to the development of methods that can make inferences under conditions of extreme observational uncertainty. Royer (Collecte Localisation Satellites, France) demonstrated how Bayesian filtering was applied to the analysis of marine turtle logger data, enabling separate quantification of the uncertainty in movement and observation processes and providing a clearer picture of uncertainty in habitat use (Royer & Lutcavage 2008). Struve (Imperial College) outlined how Bayesian inference in combination with a biased random walk model can be used to extract within-patch and inter-patch movements of marine fishes from acoustic telemetry data, also shedding light on uncertainty in the relative importance of different coastal habitats.

(b) Populations

Density-dependent habitat selection based on the ideal free distribution (IFD; Fretwell & Lucas 1970) is a key process that links individual movement, habitat suitability and population dynamics. In his keynote address, MacCall (NOAA, USA) revisited the basin model (MacCall 1990), which, using the idea of the IFD, compares the density distribution of a population within its geographical range to the behaviour of a viscous liquid in a basin, whose depth serves as a quantitative metaphor for local habitat suitability. Intrinsic habitat quality increases from the periphery to the

centre of the geographical range, but realized habitat suitability is reduced owing to the effect of local conspecific density. The underlying dynamics of the basin model include density-dependent population growth, mortality, diffusion and a migration flux that is proportional to the gradient in realized habitat suitability. The basin model predicts a range of population behaviours that can be tested against field observations, for example, contraction and expansion of the geographical distributions in response to changes in population abundance, correlation between local density and resource availability and hysteresis. Such relationships are widely observed both in terrestrial and aquatic environments (Beckmann & Berger 2003; Barange *et al.* 2009).

Often, habitat suitability is inferred from density distributions, which leads to circularity in distribution and population models. Blanchard (Imperial College) demonstrated that habitat suitability could be derived independently of density distribution observations. A simple IFD model linking sea-floor temperature, temperature-dependent growth rate and population abundance to habitat quality was consistent with observed patterns in the geographical distribution of juvenile North Sea cod (*Gadus morhua*) over time (Blanchard *et al.* 2005).

Within a management context, understanding the overall spatial distribution of a population can negate the need for detailed representations of individual movement. Furthermore, it is often the only inference that can be made given limitations in the data, particularly for the marine environment. Edwards (Imperial College) presented a model that could estimate the biomass distribution at age from marine fisheries data, and applied it to assess the consequences of different spatial management scenarios.

Spatially explicit population dynamics models can reveal the influence of individual movement and dispersal on the long-term population trajectories. Ozgul (Imperial College) used a stage-based, spatially explicit matrix projection model to illustrate the relative influence of dispersal and local population dynamics on the dynamics of a marmot (*Marmota flaviventris*) metapopulation (Ozgul *et al.* 2009). Dispersal behaviour, obtained from radio-telemetry data, redistributes young individuals among the patch network, where local dynamics are governed by survival and reproduction within patches. While short-term regional dynamics were most influenced by dispersal and spatial structure, long-term dynamics were mainly influenced by population processes within high-quality sites.

(c) Species ranges

Modelling of species' ranges and geographical distributions is important where simple mapping will not do: when observation coverage is incomplete, and in order to understand range shifts associated with environmental change. Yesson (Zoological Society London, UK) pointed out the potential benefits of empirical species distribution models (SDM) for estimating the spatial distributions of species that, owing to practical and financial limitations, are difficult to sample, such

as deep-water corals. Hortal (Imperial College) highlighted the fact that poor data (in terms of quality and coverage) are often used to generate SDM and suggested that spatially explicit descriptions of bias and uncertainty accompany species distribution maps.

The subsequent discussion addressed how dynamic population processes affect observed empirical associations between species and habitats. Empirical SDM identify potentially suitable areas from existing distributions, by extrapolating across time, space and populations. Historical effects, data incompleteness, individual variability and transient and spatial population processes introduce uncertainty into such relationships. The use of SDM for extrapolations to new climate conditions, regions or genetically distinct populations is thus questionable (Kearney 2006). It has been suggested that mechanistic niche models will produce more reliable projections of range shifts under new conditions (Kearney & Porter 2009).

3. DIRECTIONS: LINKING LEVELS AND APPROACHES

Different observation and modelling approaches are used in understanding and predicting spatial dynamics at individual, population and species level. Although the relative importance of the basic determinants of species distributions vary across scales (Hortal *et al.* 2010), the basic concepts of niche (relationship between environmental factors and fitness), spatial variation in environments and dispersal underlie spatial ecology at all levels (Holt 2003). Links are also given by underlying ecological-evolutionary theory. The interaction of population processes, dispersal and evolutionary change determine the dynamics of species' ranges. Linking spatial distributions to processes at the individual, population and metapopulation level provides insights into their potential response to environmental change.

Cross-level analysis is critical to understanding processes that determine the spatial behaviour of individuals and populations. Terrestrial studies, because of the relative ease of accurate census and detailed long-term observation, can reveal the consequences of individual behaviour for population trajectories and range dynamics at a level of detail that is difficult to achieve with organisms that are largely invisible. Studies on the spatial behaviour of fish populations provide insights into processes that lead to population-wide response to climate change, and ultimately, to global changes in biodiversity (Cheung *et al.* 2009). They also hold the key to breaking the circularity immanent in many habitat–distribution modelling approaches where habitat suitability is inferred from observed distributions.

Marine and terrestrial scientists face similar challenges when dealing with large observational errors and uncertainty in underlying process dynamics. Linking levels and approaches will help in developing predictive models, using methods developed in both scientific realms to fill gaps in distribution maps and possibly allowing separation of process and observation

uncertainties. State space models accomplish this feat. Widely used in fisheries science, they have recently been discovered for animal movement models (reviewed in Patterson *et al.* 2008), and may fruitfully be applied at other levels and in other systems.

The species–habitat associations that we observe and model are continually re-shaped by dynamic ecological and evolutionary processes which can feedback across levels of organization. Anthropogenic and environmental changes are also occurring and driving changes at similar time scales. Improved connectivity of data and theory across all levels of organization will only help in our ability to understand and predict the consequences.

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