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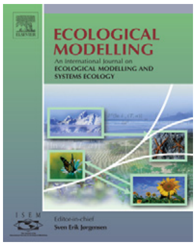

Short communication

Patterns for parameters in simulation models

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ABSTRACT

Population simulation models are often used in conservation biology to assess human impact on species survival, but have been under heavy critique due to parameterization problems. The general notion is that only models for which parameters were directly assessed from field data can show that a certain process is working, in contrast to using field data to fit models. We would like to provide an update regarding the relationship between simulation model parameterization and the use of field data as 'pattern' for revealing 'structurally realistic' parameters and processes. 'Pattern-oriented modelling' is an inverse modelling technique in ecology that considers the use of multiple field data pattern simultaneously to filter the parameterizations which were successfully tested against all available data on system dynamics. We highlight this technique with an example of our own research and conclude that this approach is especially suitable for models in conservation of rare and elusive species, where data are generally scarce.

The assessment of human impact on the survival of species, such as fragmentation due to roads or landscape changes, increasingly relies on population viability analyses (PVA), which use demographic models incorporating various aspects of the ecology and behaviour of the species (Akcakaya and Raphael, 1998; Beissinger and McCullough, 2002; Boyce, 1992). Because the relevant biology is in general complex, simulation models of intermediate complexity are virtually the only means of finding an answer for distinct questions of population development under different landscape and demographic scenarios (DeAngelis and Mooij, 2003). However, these models have been under heavy critique because of their 'immense' data requirements, and particularly because of problems associated with model parameterization, i.e., because it is usually impossible to derive direct field estimates for many model parameters (Beissinger and Westphal, 1998; Doak and Mills, 1994). A dominant belief in ecology which has its roots in regression analysis is that only models for which the parameters of underlying processes were estimated independently (i.e., directly from the data) can prove that a certain mechanism is operating (Beissinger, 1995; Beissinger and Westphal, 1998; deRoos et al., 1992; Huisman and Sommeijer, 2002; McCauley et al., 1993,1996; Peck, 2004). The notion behind this belief in independence is that models that were *fitted* to observations are not reliable because the addition of parameters may increase the ability of models to fit the observations without guaranteeing that a model which fits the observations better contains the "correct" processes and parameters.

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This notion is correct in principle (and well known in statistical modelling) but ignores both recent advances in ecological modelling and established techniques of indirect parameterization in other disciplines. Direct field estimates are not the only means of parameterizing a model. We think that the potential of parameterizing simulation models is underestimated in the ecological literature. Here, we would like to provide a brief update regarding the use of patterns for selecting parameters and processes in simulation models.

Specific techniques are available that can be used in simulation modelling to indirectly parameterize simulation models. These so-called 'inverse modelling' techniques (Bennett, 2002; Gottlieb and DuChateau, 1996; Tarantola, 1987) are used in many areas of science, e.g., in hydrology, geology, soil science, oceanography, or global climate modelling, but rarely in ecology. Generally, we have better data on system responses than on the processes and parameters that drive those responses. Inverse modelling estimates optimal parameter values by optimizing the match between observed system responses and the corresponding simulated responses. In ecology, 'pattern-oriented modelling' (Grimm et al., 2005, 1996; Grimm and Railsback, 2005; Wiegand et al., 2003, 2004) is a modelling technique which can be combined with techniques of inverse modelling for indirect parameter estimation. However, the difference to inverse modelling is that pattern-oriented modelling uses *multiple* patterns (data), each describing a certain characteristic aspect of the real system. An accepted parameterization must simultaneously produce simulation results with small departures in all patterns. With these techniques one can use patterns observed at several hierarchical levels (e.g., population scale patterns such as time series data of population counts or spatial distribution patterns, descriptive statistical analyses of field data like daily distance distributions, etc.) to simultaneously estimate model parameters which operate at different hierarchical levels (e.g., demographic parameters such as mortality probability which act on the individual level).

Under the pattern-oriented technique, observed patterns are used to hypothesize a model structure by asking what parameters and processes must be included in the model so that these patterns could, in principle, emerge (Grimm et al., 2005). Then, the comparison of model output and observed patterns can be used for two purposes. First, patterns can be used for parameterization. All unknown parameters are varied systematically over the entire parameter space, and multiple patterns observed at different scales and hierarchical levels can be used to determine multiple parameters (Wiegand et al., 2004). Second, patterns can be used to select the most appropriate submodels of certain processes. The question is which of the alternative submodels that we specified is capable of reproducing all observed patterns simultaneously (Railsback, 2001; Railsback and Harvey, 2003). This is an important control mechanism to detect wrong model structures and to yield 'structurally realistic' (Grimm et al., 2005; Wiegand et al., 2003) models. The more different features of the system are successfully tested, the less likely it is that the model structure or parameterization is wrong. Thus, using multiple patterns, not only one, is very important, but can also be fairly data intensive. While it might be relatively simple to reproduce one feature of a system, the simultaneous fulfilment of several patterns describing different features is by far non-trivial (Levin et al., 1997; Wiegand et al., 2003; Revilla et al., 2004). Furthermore, as many processes may not be known that work on a lower hierarchical level than the observations, e.g., dispersal behaviour, alternative hypotheses of these low-level processes can be tested in the full model (Kramer-Schadt et al., 2004).

Generally, the outcome of an indirect pattern-oriented parameterization will not be one 'optimum' parameterization but an entire 'cloud' in parameter space. This is because of uncertainties in the data and the model structure, and we have to accept it as remaining uncertainty not reducible with the current data. As parameters are simultaneously estimated, this method considers possible trade-offs or interactions between model parameters which may cause severe problems of error propagation in conventional parameterization (Wiegand et al., 2003).

Let us illustrate the method of pattern-oriented modelling and parameterization with a typical example from conservation biology, where direct estimates of the parameters (i.e., high parameter uncertainty) as well as knowledge about the processes (i.e., high structural uncertainty) are lacking. To assess the impact of road mortality on patch connectivity for lynx in Germany, Kramer-Schadt et al. (2004) needed to parameterize an individual-based dispersal model, where information on the actual movement path within the active period was needed, but only data on the day-to-day level were available. To tackle this problem, Kramer-Schadt et al. (2004) derived a model to simulate the dispersal of individual lynx exactly as observed during the telemetric study, i.e., with their individual time span of dispersal (dispersal season) and released on a habitat suitability map in the same place where the real lynx had started dispersal. Thus, they could ignore any demographic processes like mortality, because there was no mortality in the field data.

The unknown *processes* were, whether lynx prefer a certain direction depending on the type of habitat surrounding them, and whether they keep a certain direction. Kramer-Schadt et al. (2004) developed four nested movement models, a random walk (RW), a correlated random walk (CRW), where the direction within a day was kept with a certain probability, a habitat dependent walk (HDW) with different probabilities to prefer suitable habitat, and a correlated habitat dependent walk (CHDW), where the hierarchy was suitable habitat before keeping the direction (Table 1). RW is the simplest movement type nested in the other movement types which contain additional processes and parameters.

The unknown *parameters* were, how many steps each lynx moves within 1 day, which direction the lynx takes at each step, the probability to leave suitable habitat per step, and with that the number of steps spent in unsuitable habitat. These parameters were varied over a wide range and implemented in each of these movement models, e.g., the probability to leave dispersal habitat ranged between 0 and 1 in the habitat dependent models, and the number of steps per day was drawn within a biologically meaningful range in all models.

From the lynx' field data set four patterns were derived for comparison with the simulated data: (1) the habitat use of dispersing lynx, (2) the average maximum distance of the seasonal dispersal of all lynx, (3) the fact that they stayed within a given area and (4) the daily step distribution (Table 1). Finally,

Table 1 – Parameterization of the lynx dispersal model for the movement types random walk (RW), correlated random walk (CRW), habitat dependent walk (HDW) and correlated habitat dependent walk (CHDW)

Movement type	*n* Simulation runs	Pattern performance [%]				Simultaneous fit of all 4 patterns [%]
		Pattern 1 habitat use	Pattern 2 average maximum distance	Pattern 3 study area	Pattern 4 step distribution	
RW	70	0	59	3	26	0
CRW	700	0	60	4	25	0
HDW	840	76	45	58	26	11 ($n = 90$)
CHDW	8400	86	56	46	37	18 ($n = 1535$)

The increase in simulation runs for the movement types is due to their nested structure, i.e., HDW is based on RW but has one variable more which is multiplied with the other variables to scan the whole parameter space. Each parameter set was repeated 100 times in each simulation run, and the mean of the 100 repetitions was compared with the observed patterns (see below; Kramer-Schadt et al., 2004). Only when including a preference for dispersal habitat (HDW, CHDW), all patterns were performed simultaneously.

Pattern1 'Habitat Use': This pattern refers to the frequency of dispersal habitat use during the observation period. We used replacement techniques to define the range of the observed habitat use and designated the pattern as satisfied when the mean of the simulated pattern was above 81%. Pattern 2 'Average Maximum Distance' refers to the maximum net distance from the starting point of dispersal. We defined the pattern as replicated when the observed value of 41.7 km was inside the envelope (mean ± S.D.) of the simulation. Pattern 3 'Study Area': We defined this pattern to be fulfilled when simulated lynx stayed within the area known to host lynx. Pattern 4 'Step Distribution': The distribution of distances at 1-km intervals follows a power function. We calculated the root of the mean squared deviation between simulated and observed distributions and, after having used resampling techniques, defined the pattern as satisfied when the squared error was below 0.037.

quantitative criteria to evaluate the agreement between these observed and simulated patterns were evaluated: when the mean of the observed pattern was within the range (e.g., one standard deviation) of the simulation runs or vice versa, the respective parameterization was evaluated to fulfil the pattern (Table 1).

The four observed patterns were used as filters to remove parameterizations not in agreement with the observations and to considerably reducing parameter uncertainty (Fig. 1). It is noteworthy that single patterns could be reproduced many times in the different movement models, but not simultaneously (Table 1), indicating that interactions among parameters are important. Thus, the random walk could be effectively rejected. Even if this indirect parameter estimate method did not result in a single best parameterization, it could reduce the number of input parameter sets substantially and assured that a model behaviour in accordance with the dispersal data was produced. The indirect approach allows for the use of more data than the conventional approach, because the field data themselves could not have been used for parameterizing the model as they were obtained at a higher hierarchical level. This is of essential importance in situations of scarce data. Our example illustrates how in general, despite sparse data, individual-based models can be successfully developed, parameterized, and applied to real ecological management problems. This approach could be useful for a variety of models from ecological research (Hancock et al., 2005; Jopp and Reuter, 2005; Mathevet et al., 2003; Reuter, 2005; Yamanaka et al., 2003).

We conclude, that pattern-oriented modelling can be used for detecting the underlying processes that reproduce the observed patterns as well as plausible parameterizations, and inferences can be made from more aggregated data to processes working on a lower level or vice versa. Data are thus not only included from previous studies to construct the model itself, as stated by Peck (2004), but the data themselves contain 'hidden information' (Wiegand et al., 2003), which can

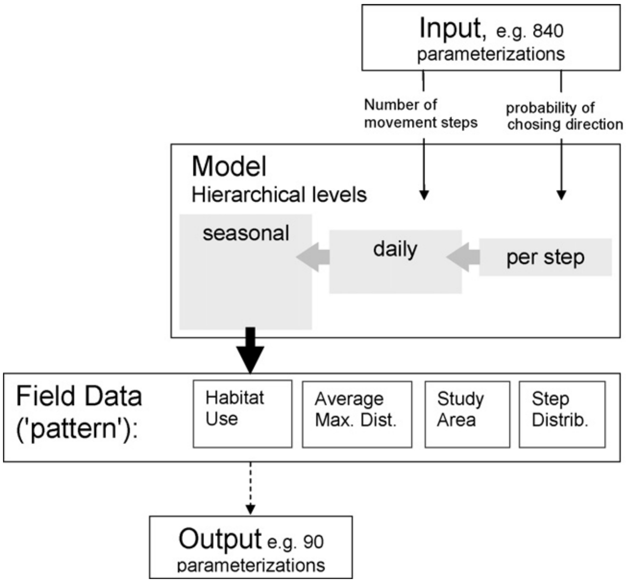

Fig. 1 – Structure of the lynx dispersal model with processes working at different hierarchical scales. As an input we get many parameterizations (symbolized as thin arrows) of the unknown process taking place at the lowest model level (per step). The results of the lower model levels (per step, daily) are aggregated to the higher level (grey arrows). At a higher hierarchical level, e.g., after each dispersal season (seasonal), the model results are measured (thick arrows) in accordance with the field data, that act as multiple filters on the seasonal level. Only parameterizations that simultaneously fulfil all patterns are accepted, reducing the input parameter set (thin dashed arrows).

be revealed by this method. Thus, this approach is especially suitable for models in conservation of rare or elusive species, where data generally are scarce and messy, and where any information about the system is valuable (Rossmanith et al., 2007; Wiegand et al., 2003, 2004).

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