Coming out of the ivory tower: how to ensure that ecological modelling research remains practical and applied

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Thirty PhD students and postdocs from seven countries came together for the 'Populations Under Pressure' symposium, held in March 2007 at the NERC Centre for Population Biology situated at Imperial College London's Silwood Park campus. The symposium aimed to stimulate interdisciplinary discussion on topical and emerging issues in applied population biology, with a focus on conservation.



Delegates to the Populations under Pressure symposium

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Interdisciplinary research is becoming increasingly popular and has been shown to stimulate new lines of research (Holt and Webb 2007). Indeed many funding bodies and advertised faculty jobs state outright a preference for research that spans two or more disciplines. One of the consequences is that many ecology PhD students and early career researchers are nowadays seeking to include a modelling component in their work, with a view to broadening their skills. During the symposium, two key themes emerged from the discussions: how to choose the appropriate level of model complexity to describe our system, and how to communicate effectively our results outside of academia, particularly in the context of shaping conservation policy.

## The appeal of complexity

While modelling by ecologists is helpful to sharpen thinking and understand the study system, there is an alarming tendency among researchers inexperienced in the domain for inappropriate use of complex simulation models and 'black box' packages, in which a relatively large number of input parameters are used to generate outputs such as extinction risks (Coulson et al 2001), habitat use (Manly et al. 2002), or population growth (Lande et al. 2003). Identifying the key processes driving population or community dynamics from parameter-rich simulation models can be extremely difficult given the variability in the estimates of input parameters (which can be caused by low precision of parameter estimates or by models with exceedingly large numbers of parameter combinations). Another common issue is whether the model should contain only additive effects or also interaction terms; as in biology the latter might often be more appropriate. Furthermore, incomplete descriptions of complex models in the published literature often impede the reproducibility of the models by other researchers, as well as a critical evaluation of the ecological relevance of the model results. Finally, excessive data requirements by complex models prevent tests with real data because the feasibility of applying the required sampling design becomes very low.

All researchers considering building a model should first of all ask themselves whether their research question really merits a model. No model, no matter how complex, can hope to exactly mirror biological phenomena, and the value of simple models should not be underestimated (Levins 1966). Indeed, even for complex models the aim is not "realism" but using a tool to answer a research question (Mangel et al. 2001; Kokko 2005). Simple models offer conceptual clarity, which helps the researcher in framing the research questions and facilitates the comprehension of the results by the target audience once

the research is published. Starting out with simple caricature models provides a good opportunity to build a solid grounding in ecological theory and can provide a justification for a more complex approach if the simple models fail to explain the qualitative behaviour of the observed system. Nevertheless, it is crucial that more complex models are rooted in, and their results interpreted based on, general ecological theory (see also Grimm et al. 2005, 2006). In fact, the lack of orientation towards more general (theoretical) issues is one of the main critiques of complex models.

The results obtained from simple models can highlight key conceptual faults before a series of time-expensive simulations is carried out, just as pilot studies are undertaken before a large-scale experiment is started. For example, Ludwig & Walters (1985) used a relatively complex age-structured model to generate a dataset, and then used this dataset to compare the predictive power of the generating model against a simple lumped population model. The simple model performed better, even though it had not been used to generate the data, because of correlations among parameters, especially when they were estimated from a limited amount of data.

Complexity vs. simplicity: let the data speak One crucial point in the discussion was how to improve the speed at which we make progress. One central question in that context is the extent to which this is achieved by building increasingly complex models, or rather by spending more time with the computer shut down (i.e. thinking more, reading more) - and using the time to come up with simple, general and testable hypotheses that do not require complex statistical models or ad hoc inductive reasoning (see also Peck 2004). Or would the latter only result in us abandoning all the data that are not sampled in a way that is ideal to test a specific hypothesis? Until recently there has been a trade-off between having "ideal" data on a limited number of taxa, and poor quality data on a large range of taxa. An obvious example is given by studies on population growth. Future methodological progress should aim at including simultaneously both kinds of information rather than trying to compensate for the lack of information (too few data or poor quality data) by an increasingly complex modelling approach.

Furthermore, a contentious issue is how to distinguish a complex from a simple model. Should the level of complexity be interpreted in terms of the number of parameters or how well we understand the underlying assumptions (and output) from simulation models? The principle of parsimony is a good

working guideline (Young et al 1996) – in Einstein's words: keep things as simple as possible, but no simpler. However, it is often a matter of discussion what simple and complex means (in some cases it is simple to see, in other cases we find it more questionable). For example, is complex a synonym for "complicated"? We stress it is not. A complex model could be easy to understand if based on a solid and clear ecological background.

One important point that is overlooked in ecology nowadays, and that could guide us when debating complexity vs. simplicity, is the suggestion by Hilborn and Mangel (1997; and similarly already advocated by Tukey 1977): "Always plot your data". Visual display of the data might be of invaluable help to check assumptions prior to our analyses (Cleveland 1993). One can be sure that the combination of thinking and analysis required for this leads to something that can be understood and easily communicated to a wide range of people within a more complex framework (as humans have very good visual abilities). Indeed, showing the data, and not only the models, should become a routine practice in scientific papers. By this we might be able to identify the most important, clearest and effective components of our analysis without the need to communicate all details of our model. However, one should also keep in mind the remark generally attributed to Kruskal that most data sets have 2.5 dimensions: two that can be shown in a printed plot, and something extra that needs to be explained in the text.

# How to stay applied? Forget you're a scientist!

The question arose of how the points discussed above help us to make sure that our efforts remain applied and practical. There are two different types of application of our research efforts. One is where scientists stay within their scientific world and use the available tools to answer applied questions. Another is where science leads to recommendations for management (especially in the context of conservation or exploitation of target populations) and communication of scientific work to a non-scientific audience.

Science for its own sake is important and needs to be rigorous, but is often irrelevant to managers because results are too complex, costly or unethical to be put in action – or, this is how they are frequently perceived. In addition, often there is a mismatch between the questions investigated by researchers, and the actual problems managers of natural resources are facing. Hence, the ability to share interdisciplinary experience and expertise with practitioners

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and managers can generate hypothesis testing that is directly linked to practical problems. For example, the population dynamics of many vertebrates are well studied; however, the direct question of most managers is how human impacts and the ecology of the species interact and how to adjust management accordingly. For example, in sexually dimorphic ungulates like red deer, sex differences in demographic parameters might have to be considered in order to maximise the income from trophy hunting (Clutton-Brock et al. 2002, Gaillard et al. 2003). Furthermore the management regime of one estate might affect the composition and dynamics of neighbouring estates as the movement of individuals are interlinked (Milner-Gulland et al. 2004).

Frequent interdisciplinary contact with non-scientists would also help us in becoming better communicators, as it forces us to get out of our ivory tower and learn to communicate without speaking our "secret language" - e.g. avoiding specific terms of our discipline and avoiding using statistics as if it was our native language (Sand-Jelen 2007). If we want to communicate our findings, the worst thing would be to reduce them to a number, even if we call it p-value; visual displays are often more effective.

In conclusion, our aim here is to advocate the pedagogic and conceptual value of starting out simply in modelling, and gradually adding in complexity. Furthermore, interdisciplinary interactions with practitioners are crucial to ensure our work will be relevant and applicable to real-world situations. This combined approach will also help us in communicating effectively our results outside of academia, particularly in the context of shaping conservation policy.

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