

Scientific publications with ODD model descriptions

Supplemental material for Exercise 1, Chapter 3 of *Agent-Based and Individual-Based Modeling*

Acerbi, A., P. McNamara, and C. Nunn. 2008. To sleep or not to sleep: the ecology of sleep in artificial organisms. *BMC Ecology* 8:10. <http://www.biomedcentral.com/1472-6785/8/10>

All animals thus far studied sleep, but little is known about the ecological factors that generate differences in sleep characteristics across species, such as total sleep duration or division of sleep into multiple bouts across the 24-hour period (i.e., monophasic or polyphasic sleep activity). Here we address these questions using an evolutionary agent-based model. The model is spatially explicit, with food and sleep sites distributed in two clusters on the landscape. Agents acquire food and sleep energy based on an internal circadian clock coded by 24 traits (one for each hour of the day) that correspond to "genes" that evolve by means of a genetic algorithm. These traits can assume three different values that specify the agents' behavior: sleep (or search for a sleep site), eat (or search for a food site), or flexibly decide action based on relative levels of sleep energy and food energy. Individuals with higher fitness scores leave more offspring in the next generation of the simulation, and the model can therefore be used to identify evolutionarily adaptive circadian clock parameters under different ecological conditions. Results We systematically varied input parameters related to the number of food and sleep sites, the degree to which food and sleep sites overlap, and the rate at which food patches were depleted. Our results reveal that: (1) the increased costs of traveling between more spatially separated food and sleep clusters select for monophasic sleep, (2) more rapid food patch depletion reduces sleep times, and (3) agents spend more time attempting to acquire the "rarer" resource, that is, the average time spent sleeping is positively correlated with the number of food patches and negatively correlated with the number of sleep patches. "Flexible" genes, in general, do not appear to be advantageous, though their arrangements in the agents' genome show characteristic patterns that suggest that selection acts on their distribution. Conclusion Collectively, the output suggests that ecological factors can have striking effects on sleep patterns. Moreover, our results demonstrate that a simple model can produce clear and sensible patterns, thus allowing it to be used to investigate a wide range of questions concerning the ecology of sleep. Quantitative data presently are unavailable to test the model predictions directly, but patterns are consistent with comparative evidence from different species, and the model can be used to target ecological factors to investigate in future research.

Bailleul, F., V. Grimm, C. Chion, and M. Hammill. 2013. Modeling implications of food resource aggregation on animal migration phenology. *Ecology and Evolution* 3:2535-2546. <http://dx.doi.org/10.1002/ece3.656>

The distribution of poikilotherms is determined by the thermal structure of the marine environment that they are exposed to. Recent research has indicated that changes in migration phenology of beluga whales in the Arctic are triggered by changes in the thermal structure of the marine environment in their summering area. If sea temperatures reflect the spatial distribution of food resources, then changes in the thermal regime will affect how homogeneous or clumped food is distributed. We explore, by individual-based modelling, the hypothesis that changes in migration phenology are not necessarily or exclusively triggered by changes in food abundance, but also by changes in the spatial aggregation of food. We found that the level of food aggregation can significantly affect the relationship between the timing of the start of migration to the winter grounds and the total prey capture of individuals. Our approach strongly indicates that changes in the spatial distribution of food resources should be considered for understanding and quantitatively predicting changes in the phenology of animal migration.

Chen, X., F. Lupi, L. An, R. Sheely, A. Viña, and J. Liu. 2012. Agent-based modeling of the effects of social norms on enrollment in payments for ecosystem services. *Ecological Modelling* 229:16-24.

<http://www.sciencedirect.com/science/article/pii/S0304380011003401>

Conservation investments are increasingly being implemented through payments for ecosystem services (PES) for the protection and restoration of ecosystem services around the world. Previous studies suggested that social norms have substantial impacts on environmental behaviors of humans, including enrollment of PES programs. However, it is still not well understood how social norms are affected by the design of PES programs and how the evolution of social norms may affect the efficiency of conservation investments. In this paper, we developed an agent-based simulation model to demonstrate the evolution and impacts of social norms on the enrollment of agricultural land in a PES program. We applied the model to land plots that have been enrolled in China's Grain-to-Green Program (GTGP) to examine reenrollment in an alternative payment program when the current payments ceased. The study was conducted in Wolong Nature Reserve where several thousand plant and animal species, including giant pandas, may benefit from the reenrollment. We found that over 15% more GTGP land can be reenrolled at the same payment if social norms were leveraged by allowing more than 10 rounds of interactions among landholders regarding their reenrollment decisions. With only three rounds of interactions, an additional 7.5% GTGP land was reenrolled at the same payment due to the effects of social norms. In addition, the effects of social norms were largest at intermediate payments and were smaller at much higher or much smaller payments. Even in circumstances where frequent interactions among landholders about their enrollment decisions are not feasible, policy arrangements that divide households into multiple waves for sequential enrollment can enroll over 11% more land at a given payment level. The approach presented in this paper can be used to improve the efficiency of existing PES programs and many other conservation investments worldwide.

Conner, M. M., M. R. Ebinger, and F. F. Knowlton. 2008. Evaluating coyote management strategies using a spatially explicit, individual-based, socially structured population model. *Ecological Modelling* 219:234-247.

Managing canid predation on livestock is the leading challenge facing canid conservation worldwide. However, removing canids, and coyotes in particular, to reduce livestock predation is environmentally and socially controversial. In addition, it can be expensive and logistically difficult to field evaluate the myriad of potential selective, spatial, and temporal canid management strategies. Here, we develop a spatially explicit, individual-based simulation model to evaluate commonly used or promoted coyote control strategies. We began with an already constructed non-spatial, individual-based stochastic coyote population model that incorporated behavioral features, such as dominance and territoriality. We added a spatial component and enhanced the social rule set to more realistically model coyote movement and territory replacement. This model merges coyote spatial, social, and population ecology into a management framework. The development, structure, and parameterization of this model are described in detail. For lethal methods, model results suggest that spatially intensive removals are more efficient and long lasting compared to random removal methods. However, sterilization appears to be the management strategy offering the largest and most lasting impact on coyote population dynamics. We recommend adding spatial prey/livestock density and environmental components to this model to further enhance its ecological reality and management usefulness. Although this model is applied to coyotes in particular, it is applicable to many canid species of conservation concern. This model provides a tool to assist in the development of more effective and socially acceptable livestock predation management strategies. (C) 2008 Elsevier B.V All rights reserved

dos Santos, F. S., K. Johst, A. Huth, and V. Grimm. 2010. Interacting effects of habitat destruction and changing disturbance rates on biodiversity: Who is going to survive? *Ecological Modelling* 221:2776-2783.

<http://www.sciencedirect.com/science/article/pii/S030438001000400X>

Changes in disturbance rates due to climate change may increase or decrease diversity, whereas permanent loss of habitat is generally believed to decrease diversity. It is, however, very likely that the effects of disturbances and habitat destruction interact. Understanding such combined effects is essential to predict the response of communities to global changes and in particular which functional types of species are most endangered. Using an individual-based spatially explicit community model, we investigate (1) whether diversity–disturbance curves alter when spatially uncorrelated or autocorrelated habitat destruction is added, and (2) which functional types of species are able to survive under these altered conditions. Model communities consisted of four functional types of species trading off between colonisation ability and competition strength. We found that habitat destruction may alter both height and shape of diversity–disturbance curves: maximum diversity at intermediate disturbance rates may shift to other disturbance rates or even split into two peaks giving rise to bimodal diversity–disturbance relationships with different sub-communities persisting at low and high disturbance rates. Diversity responded differentially depending on how the colonisation–competition trade-off was represented. Our results suggest that, for trade-offs in seed production rate, generally the best coloniser will better withstand the interacting effects of habitat destruction and changing disturbance rates; however, for trade-offs in mean dispersal distances, functional types characterized by intermediate abilities will perform best. We conclude that predictions of the impacts of changing disturbance rates on biodiversity depend on community structure and cannot be made without knowledge of concurrent permanent habitat destruction.

Gabsi, F., M. Hammers-Wirtz, V. Grimm, A. Schäffer, and T. G. Preuss. Coupling different mechanistic effect models for capturing individual- and population-level effects of chemicals: Lessons from a case where standard risk assessment failed. *Ecological Modelling*. <http://www.sciencedirect.com/science/article/pii/S0304380013003025>

Current environmental risk assessment (ERA) of chemicals for aquatic invertebrates relies on standardized laboratory tests in which toxicity effects on individual survival, growth and reproduction are measured. Such tests determine the threshold concentration of a chemical below which no population-level effects are expected. How well this procedure captures effects on individuals and populations, however, remains an open question. Here we used mechanistic effect models, combining individual-level reproduction and survival models with an individual-based population model (IBM), to understand the individuals' responses and extrapolate them to the population level. We used a toxicant (Dispersogen A) for which adverse effects on laboratory populations were detected at the determined threshold concentration and thus challenged the conservatism of the current risk assessment method. Multiple toxicity effects on reproduction and survival were reported, in addition to effects on the F1 generation. We extrapolated commonly tested individual toxicity endpoints, reproduction and survival, to the population level using the IBM. Effects on reproduction were described via regression models. To select the most appropriate survival model, the IBM was run assuming either stochastic death (SD) or individual tolerance (IT). Simulations were run for different scenarios regarding the toxicant's effects: survival toxicity, reproductive toxicity, or survival and reproductive toxicity. As population-level endpoints, we used population size and structure and extinction risk. We found that survival represented as SD explained population dynamics better than IT. Integrating toxicity effects on both reproduction and survival yielded more accurate predictions of population effects than considering isolated effects. To fully capture population effects observed at high toxicant concentrations, toxicity effects transmitted to the F1 generation had to be integrated. Predicted extinction risk was highly sensitive to the assumptions about individual-level effects. Our results demonstrate that the endpoints used in current standard tests may not be sufficient for assessing the risk of adverse effects on populations. A combination of laboratory population experiments with mechanistic effect models is a powerful tool to better understand and predict effects on both individuals and populations. Mechanistic effect modelling thus holds great potential to improve the accuracy of ERA of chemicals in the future.

Giske, J., S. Eliassen, Ø. Fiksen, P. J. Jakobsen, D. L. Aksnes, C. Jørgensen, and M. Mangel. 2013. Effects of the emotion system on adaptive behavior. *American Naturalist* 182. (ODD description is in the appendix) <http://www.jstor.org/stable/10.1086/673533>

A central simplifying assumption in evolutionary behavioral ecology has been that optimal behavior is unaffected by genetic or proximate constraints. Observations and experiments show otherwise, so that attention to decision architecture and mechanisms is needed. In psychology, the proximate constraints on decision making and the processes from perception to behavior are collectively described as the emotion system. We specify a model of the emotion system in fish that includes sensory input, neuronal computation, developmental modulation, and a global organismic state and restricts attention during decision making for behavioral outcomes. The model further includes food competition, safety in numbers, and a fluctuating environment. We find that emergent strategies in evolved populations include common emotional appraisal of sensory input related to fear and hunger and also include frequency-dependent rules for behavioral responses. Focused attention is at times more important than spatial behavior for growth and survival. Spatial segregation of the population is driven by personality differences. By coupling proximate and immediate influences on behavior with ultimate fitness consequences through the emotion system, this approach contributes to a unified perspective on the phenotype, by integrating effects of the environment, genetics, development, physiology, behavior, life history, and evolution.

Grimm, V., et al. 2006. A standard protocol for describing individual-based and agent-based models. *Ecological Modelling* 198:115-126. (19 example model descriptions are in the online appendix)

Simulation models that describe autonomous individual organisms (individual based models, IBM) or agents (agent-based models, ABM) have become a widely used tool, not only in ecology, but also in many other disciplines dealing with complex systems made up of autonomous entities. However, there is no standard protocol for describing such simulation models, which can make them difficult to understand and to duplicate. This paper presents a proposed standard protocol, ODD, for describing IBMs and ABMs, developed and tested by 28 modellers who cover a wide range of fields within ecology. This protocol consists of three blocks (Overview, Design concepts, and Details), which are subdivided into seven elements: Purpose, State variables and scales, Process overview and scheduling, Design concepts, Initialization, Input, and Submodels. We explain which aspects of a model should be described in each element, and we present an example to illustrate the protocol in use. In addition, 19 examples are available in an Online Appendix. We consider ODD as a first step for establishing a more detailed common format of the description of IBMs and ABMs. Once initiated, the protocol will hopefully evolve as it becomes used by a sufficiently large proportion of modellers.

Gusset, M., O. Jakoby, M. S. Müller, M. J. Somers, R. Slotow, and V. Grimm. 2009. Dogs on the catwalk: Modelling re-introduction and translocation of endangered wild dogs in South Africa. *Biological Conservation* 142:2774-2781. <http://www.sciencedirect.com/science/article/pii/S0006320709003115>

In South Africa, a plan was launched to manage separate sub-populations of endangered African wild dogs (*Lycaon pictus*) in several small, geographically isolated conservation areas as a single meta-population. This intensive management approach involves the re-introduction of wild dogs into suitable conservation areas and periodic translocations among them. Despite the initial failures and high costs associated with wild dog re-introductions and translocations, there is no predictive framework available to quantify which management protocol is the most efficient. We therefore developed an individual-based model of wild dog population and pack dynamics, which accounts for the wild dogs' social complexity. The model appeared to capture the essential characteristics of a real wild dog population from Hluhluwe-iMfolozi Park, South Africa and to be relatively robust to parameter uncertainty, suggesting that the model is valid enough for addressing management problems. The model enabled us to quantify a critical initial number of packs (two) and individuals per pack (six) necessary for a re-introduced wild dog population to establish itself in the release area. We also found a practically feasible intervention regime at which a re-introduced wild dog

population had the best chance of persistence: intermittently adding packs (at least every 6 years) and harvesting disperser groups (as often as every 4 years) for translocation to other release sites, without threatening the small source population. This study demonstrates that individual-based models can be a powerful decision-support tool in re-introduction planning and provides insight into how populations made up of social groups have dynamics, and ultimately persistence, determined by individual behaviour.

Heppenstall, A. J., A. T. Crooks, L. M. See, and M. Batty, editors. 2012. *Agent-Based Models of Geographical Systems*. Springer. (This book includes several chapters describing ABMs of social and social-environmental systems, using ODD.)

Jovani, R. and V. Grimm. 2008. Breeding synchrony of colonial birds: from local stress to global harmony. *Proceedings of the Royal Society B-Biological Sciences* 275:1557-1563.
<http://www.ncbi.nlm.nih.gov/pmc/articles/PMC2602658/>

Why and how birds in colonies often breed in striking synchrony is an unsolved question. In colonies, conspecific birds often destroy eggs and kill chicks, either intentionally or not. We propose that social tranquillity at the time of laying can be achieved if a bird's stress level is partly determined by the agitation of its neighbours. Moreover, we propose that this local process, together with environmental cues, can synchronize breeding between neighbours and through a whole colony. We tested our hypotheses using a generic individual-based model where the breeding predisposition of females was updated daily depending on an increase in the photoperiod (positively) and the stress level of neighbours: negatively if they were agitated, and positively otherwise. A female laid her eggs when her stress level fell to a critical value. Even giving only a low relevance to the neighbour's stress level was enough to synchronize the laying date of neighbours and also of a huge colony. Moreover, females bred in a safer environment, which is known from field studies to increase fitness. Our study highlights the power of local adaptive (individual) behaviour to create global (colony) patterns. We argue that collective patterns such as breeding synchrony in colonial birds could have simple adaptive individual-level explanations.

Lin, Y., U. Berger, V. Grimm, F. Huth, and J. Weiner. 2013. Plant interactions alter the predictions of metabolic scaling theory. *PLoS ONE* 8:e57612.
<http://dx.doi.org/10.1371/journal.pone.0057612>

Metabolic scaling theory (MST) is an attempt to link physiological processes of individual organisms with macroecology. It predicts a power law relationship with an exponent of $-4/3$ between mean individual biomass and density during density-dependent mortality (self-thinning). Empirical tests have produced variable results, and the validity of MST is intensely debated. MST focuses on organisms' internal physiological mechanisms but we hypothesize that ecological interactions can be more important in determining plant mass-density relationships induced by density. We employ an individual-based model of plant stand development that includes three elements: a model of individual plant growth based on MST, different modes of local competition (size-symmetric vs. -asymmetric), and different resource levels. Our model is consistent with the observed variation in the slopes of self-thinning trajectories. Slopes were significantly shallower than $-4/3$ if competition was size-symmetric. We conclude that when the size of survivors is influenced by strong ecological interactions, these can override predictions of MST, whereas when surviving plants are less affected by interactions, individual-level metabolic processes can scale up to the population level. MST, like thermodynamics or biomechanics, sets limits within which organisms can live and function, but there may be stronger limits determined by ecological interactions. In such cases MST will not be predictive.

Lin, Y., U. Berger, V. Grimm, and Q.-R. Ji. 2012. Differences between symmetric and asymmetric facilitation matter: exploring the interplay between modes of positive and negative plant interactions. *Journal of Ecology* 100:1482-1491.
<http://dx.doi.org/10.1111/j.1365-2745.2012.02019.x>

Facilitation (positive interaction) has received increasing attention in plant ecology over the last decade. Just as for competition, distinguishing different modes of facilitation (mutualistic, commensal or even antagonistic) may be crucial. We therefore introduce the new concept of symmetric versus asymmetric facilitation and present a generic individual-based zone-of-influence model. The model simultaneously implements different modes of both facilitation and competition among individual plants via their overlapping zone of influence. Because we consider facilitation modes as a continuum related to environmental context, we integrated this concept with the stress-gradient hypothesis (SGH) by exploring differences in spatial pattern formation in self-thinning plants along a stress gradient in our model. The interplay among modes of interaction creates distinctly varied spatial patterns along stress gradients. When competition was symmetric, symmetric facilitation (mutualism) consistently led to plant aggregation along stress gradients. However, asymmetric facilitation (commensalism) produces plant aggregation only under more benign conditions but tends to intensify local competition and spatial segregation when conditions are harsh. When competition was completely asymmetric, different modes of facilitation contributed little to spatial aggregation. Symmetric facilitation significantly increased survival at the severe end of the stress gradient, which supports the claim of the SGH that facilitation should have generally positive net effects on plants under high stress levels. Asymmetric facilitation, however, was found to increase survival only under intermediate stress conditions, which contradicts the current predictions of the SGH. **Synthesis.** Our modelling study demonstrates that the interplay between modes of facilitation and competition affects different aspects of plant populations and communities, implying context-dependent outcomes and consequences. The explicit consideration of the modes and mechanisms of interactions (both facilitation and competition) and the nature of stress factors will help to extend the framework of the SGH and foster research on facilitation in plant ecology.

Lin, Y., F. Huth, U. Berger, and V. Grimm. 2013. The role of belowground competition and plastic biomass allocation in altering plant mass–density relationships. *Oikos*. In press.
<http://dx.doi.org/10.1111/j.1600-0706.2013.00921.x>

Metabolic scaling theory (MST) predicts a ‘universal scaling law’ for plant mass–density relationships, but empirical observations are more variable. Possible explanations of this variability include plasticity in biomass allocation between the above- and belowground compartment and different modes of competition, which can be asymmetric or symmetric. Although complex interactions of these factors are likely to occur, so far the majority of modelling and empirical studies has focussed on mono-factorial explanations. We here present a generic individual-based model, which allows exploring the plant mass–density relationship in realistic settings by representing plasticity of biomass allocation and different modes of competition in the above- and belowground compartment. Plants grew according to an ontogenetic growth model derived from MST. To evaluate the behavior of the simulated plants related to the allocation patterns and to validate model predictions, we conducted greenhouse experiments with tree seedlings. The model reproduced empirical patterns both at the individual and population level. Without belowground resource limitation, aboveground processes dominated and the slopes of mass–density relationships followed the predictions of MST. In contrast, resource limitation led to an increased allocation of biomass to belowground parts of the plants. The subsequent dominance of symmetric belowground competition caused significantly shallower slopes of the mass–density relationship, even though the growth of individual plants followed MST. We conclude that changes in biomass allocation induced by belowground resource limitation explain the deviations from the mass–density relationship predicted by MST. Taking into account the plasticity of biomass allocation and its linkage to the above- and belowground competition is critical for fully representing plant communities, in particular for correctly predicting their response of carbon storage and sequestration to changing environmental conditions.

Liu, C., R. M. Sibly, V. Grimm, and P. Thorbek. 2013. Linking pesticide exposure and spatial dynamics: An individual-based model of wood mouse (*Apodemus sylvaticus*) populations in agricultural landscapes. *Ecological Modelling* 248:92-102.

<http://www.sciencedirect.com/science/article/pii/S0304380012004826>

The wood mouse is a common and abundant species in agricultural landscape and is a focal species in pesticide risk assessment. Empirical studies on the ecology of the wood mouse have provided sufficient information for the species to be modelled mechanistically. An individual-based model was constructed to explicitly represent the locations and movement patterns of individual mice. This together with the schedule of pesticide application allows prediction of the risk to the population from pesticide exposure. The model included life-history traits of wood mice as well as typical landscape dynamics in agricultural farmland in the UK. The model obtains a good fit to the available population data and is fit for risk assessment purposes. It can help identify spatio-temporal situations with the largest potential risk of exposure and enables extrapolation from individual-level endpoints to population-level effects. Largest risk of exposure to pesticides was found when good crop growth in the “sink” fields coincided with high “source” population densities in the hedgerows.

Martin, B. T., T. Jager, R. M. Nisbet, T. G. Preuss, and V. Grimm. 2013. Predicting population dynamics from the properties of individuals: a cross-level test of dynamic energy budget theory. *American Naturalist* 181:506–519.

Individual-based models (IBMs) are increasingly used to link the dynamics of individuals to higher levels of biological organization. Still, many IBMs are data hungry, species specific, and time-consuming to develop and analyze. Many of these issues would be resolved by using general theories of individual dynamics as the basis for IBMs. While such theories have frequently been examined at the individual level, few cross-level tests exist that also try to predict population dynamics. Here we performed a cross-level test of dynamic energy budget (DEB) theory by parameterizing an individual-based model using individual-level data of the water flea, *Daphnia magna*, and comparing the emerging population dynamics to independent data from population experiments. We found that DEB theory successfully predicted population growth rates and peak densities but failed to capture the decline phase. Further assumptions on food-dependent mortality of juveniles were needed to capture the population dynamics after the initial population peak. The resulting model then predicted, without further calibration, characteristic switches between small- and large-amplitude cycles, which have been observed for *Daphnia*. We conclude that cross-level tests help detect gaps in current individual-level theories and ultimately will lead to theory development and the establishment of a generic basis for individual-based models and ecology.

May, F., V. Grimm, and F. Jeltsch. 2009. Reversed effects of grazing on plant diversity: the role of below-ground competition and size symmetry. *Oikos* 118:1830-1843.

<http://dx.doi.org/10.1111/j.1600-0706.2009.17724.x>

Grazing is known as one of the key factors for diversity and community composition in grassland ecosystems, but the response of plant communities towards grazing varies remarkably between sites with different environmental conditions. It is generally accepted that grazing increases plant diversity in productive environments, while it tends to reduce diversity in unproductive habitats (grazing reversal hypothesis). Despite empirical evidence for this pattern the mechanistic link between modes of plant–plant competition and grazing response at the community level still remains poorly understood. Root-competition in particular has rarely been included in theoretical studies, although it has been hypothesized that variations in productivity and grazing regime can alter the relative importance of shoot- and root-competition. We therefore developed an individual-based model based on plant functional traits to investigate the response of a grassland community towards grazing. Models of different complexity, either incorporating only shoot competition or with distinct shoot- and root-competition, were used to study the interactive effects of grazing, resource availability, and the mode of competition (size-symmetric or asymmetric). The pattern predicted by the grazing reversal hypothesis (GRH) can only be explained by our model if shoot- and root-competition are explicitly considered and if size asymmetry of above- and

symmetry of below-ground competition is assumed. For this scenario, the model additionally reproduced empirically observed plant trait responses: erect and large plant functional types (PFTs) dominated without grazing, while frequent grazing favoured small PFTs with a rosette growth form. We conclude that interactions between shoot- and root-competition and size symmetry/asymmetry of plant-plant interactions are crucial in order to understand grazing response under different habitat productivities. Our results suggest that future empirical trait surveys in grassland communities should include root traits, which have been largely ignored in previous studies, in order to improve predictions of plants' responses to grazing.

Meli, M., A. Auclerc, A. Palmqvist, V. E. Forbes, and V. Grimm. 2013. Population-level consequences of spatially heterogeneous exposure to heavy metals in soil: An individual-based model of springtails. *Ecological Modelling* 250:338-351.
<http://www.sciencedirect.com/science/article/pii/S0304380012005479>

Contamination of soil with toxic heavy metals poses a major threat to the environment and human health. Anthropogenic sources include smelting of ores, municipal wastes, fertilizers, and pesticides. In assessing soil quality and the environmental and ecological risk of contamination with heavy metals, often homogeneous contamination of the soil is assumed. However, soils are very heterogeneous environments. Consequently, both contamination and the response of soil organisms can be assumed to be heterogeneous. This might have consequences for the exposure of soil organisms and for the extrapolation of risk from the individual to the population level. Therefore, to explore how soil contamination of different spatial heterogeneity affects population dynamics of soil invertebrates, we developed a spatially explicit individual-based model of the springtail, *Folsomia candida*, a standard test species for ecotoxicological risk assessment. In the model, individuals were assumed to sense and avoid contaminated habitat with a certain probability that depends on contamination level. Avoidance of contaminated areas thus influenced the individuals' movement and feeding, their exposure, and in turn all other biological processes underlying population dynamics. Model rules and parameters were based on data from the literature, or were determined via pattern-oriented modelling. The model correctly predicted several patterns that were not used for model design and calibration. Simulation results showed that the ability of the individuals to detect and avoid the toxicant, combined with the presence of clean habitat patches which act as "refuges", made equilibrium population size due to toxic effects less sensitive to increases in toxicant concentration. Additionally, the level of heterogeneity among patches of soil (i.e. the difference in concentration) was important: at the same average concentration, a homogeneously contaminated scenario was the least favourable habitat, while higher levels of heterogeneity corresponded to higher population growth rate and equilibrium size. Our model can thus be used as a tool for extrapolating from short-term effects at the individual level to long-term effects at the population level under more realistic conditions. It can thus be used to develop and extrapolate from standard ecotoxicological tests in the laboratory to ecological risk assessments.

Mueller, T., W. Fagan, and V. Grimm. 2011. Integrating individual search and navigation behaviors in mechanistic movement models. *Theoretical Ecology* 4:341-355.
<http://dx.doi.org/10.1007/s12080-010-0081-1>

Understanding complex movement behaviors via mechanistic models is one key challenge in movement ecology. We built a theoretical simulation model using evolutionarily trained artificial neural networks (ANNs) wherein individuals evolve movement behaviors in response to resource landscapes on which they search and navigate. We distinguished among non-oriented movements in response to proximate stimuli, oriented movements utilizing perceptual cues from distant targets, and memory mechanisms that assume prior knowledge of a target's location and then tested the relevance of these three movement behaviors in relation to size of resource patches, predictability of resource landscapes, and the occurrence of movement barriers. Individuals were more efficient in locating resources under larger patch sizes and predictable landscapes when memory was advantageous. However, memory was also frequently used in unpredictable landscapes with intermediate patch sizes to systematically search the entire spatial domain, and because of this, we suggest that memory may be important in explaining super-diffusion observed in many empirical studies. The sudden imposition of movement barriers had the greatest effect under predictable landscapes

and temporarily eliminated the benefits of memory. Overall, we demonstrate how movement behaviors that are linked to certain cognitive abilities can be represented by state variables in ANNs and how, by altering these state variables, the relevance of different behaviors under different spatiotemporal resource dynamics can be tested. If adapted to fit empirical movement paths, methods described here could help reveal behavioral mechanisms of real animals and predict effects of anthropogenic landscape changes on animal movement.

Piou, C. and E. Prévosta. 2012. A demo-genetic individual-based model for Atlantic salmon populations: model structure, parameterization and sensitivity. *Ecological Modelling* 231:37-52.

Predicting the persistence and adaptability of natural populations to climate change is a challenging task. Mechanistic models that integrate biological and evolutionary processes are helpful toward this aim. Atlantic salmon, *Salmo salar* (L.), is a good candidate to assess the effect of environmental change on a species with a complex life history through an integrative modelling approach due to (i) a large amount of knowledge concerning its biology and (ii) extensive historical data sets that can be used for model validation. This paper presents an individual-based demo-genetic model developed to simulate *S. salar* population dynamics in southern European populations: IBASAM (Individual-Based Atlantic SALmon Model). The model structure is described thoroughly. A parameterization exercise was conducted to adjust the model to an extensive set of demographic data collected over 15 years on the Scorff River, Brittany, France. A sensitivity analysis showed that two parameters determining mean and variability of juvenile growth rates were crucial in structuring the simulated populations. Additionally, realistic microevolutionary patterns of different aspects of life history were predicted by the model, reproducing general knowledge on *S. salar* population biology. The integration into IBASAM of a demo-genetic structure coupled with the explicit representation of individual variability and complex life histories makes it a cohesive and novel tool to assess the effect of potential stressors on evolutionary demography of Atlantic salmon in further studies.

Polhill, J. G., D. G. Brown, and V. Grimm. 2008. Using the ODD protocol for describing three agent-based social simulation models of land use change. *Journal of Artificial Societies and Social Simulation* 11. <http://jasss.soc.surrey.ac.uk/11/2/3.html>

This article describes three agent-based social simulation models in the area of land-use change using a model documentation protocol, ODD, from the ecological literature. Our goal is to evaluate how well fitted it is to social simulations and how successful it might be in increasing communication between individual- and agent-based modellers. Such shared protocols can facilitate model review, comparison, and replication. We initially conclude that the framework holds promise as a standard communication mechanism, although some refinements may be needed.

Premo, L. S. and J. J. Hublin. 2009. Culture, population structure, and low genetic diversity in Pleistocene hominins. *Proceedings of the National Academy of Sciences of the United States of America* 106:33-37. <http://www.pnas.org/content/106/1/33.full>

Paleogenomic research has shown that modern humans, Neanderthals, and their most recent common ancestor have displayed less genetic diversity than living great apes. The traditional interpretation that low levels of genetic diversity in modern humans resulted from a relatively recent demographic bottleneck cannot account for similarly low levels of genetic diversity in Middle Pleistocene hominins. A more parsimonious hypothesis proposes that the effective population size of the human lineage has been low for more than 500,000 years, but the mechanism responsible for suppressing genetic diversity in Pleistocene hominin populations without similarly affecting that of their hominoid contemporaries remains unknown. Here we use agent-based simulation to study the effect of culturally mediated migration on neutral genetic diversity in structured populations. We show that, in populations structured by culturally mediated migration, selection can suppress neutral genetic diversity over thousands of generations, even in the absence of bottlenecks or expansions in census population size. In other words, selection could have

suppressed the effective population size of Pleistocene hominins for as long as the degree of cultural similarity between regionally differentiated groups played an important role in mediating intraspecific gene flow.

Radchuk, V., K. Johst, J. Groeneveld, V. Grimm, and N. Schtickzelle. 2013. Behind the scenes of population viability modeling: Predicting butterfly metapopulation dynamics under climate change. *Ecological Modelling* 259:62-73.

<http://www.sciencedirect.com/science/article/pii/S0304380013001713>

Studies explaining the choice of model structure for population viability analysis (PVA) are rare and no such study exists for butterfly species, a focal group for conservation. Here, we describe in detail the development of a model to predict population viability of a glacial relict butterfly species, *Boloria eunomia*, under climate change. We compared four alternative formulations of an individual-based model, differing in the environmental factors acting on the survival of immature life stages: temperature (only temperature impact), weather (temperature, precipitation, and sunshine), temperature and parasitism, and weather and parasitism. Following pattern-oriented modeling, four observed patterns were used to contrast these models: one qualitative (response of population size to habitat parameters) and three quantitative ones describing population dynamics during eight years (mean and variability of population size, and magnitude of the temporal autocorrelation in yearly population growth rates). The four model formulations were not equally able to depict population dynamics under current environmental conditions; the model including only temperature was selected as the most parsimonious model sufficiently well reproducing the empirical patterns. We used all four model formulations to test a range of climate change scenarios that were characterized by changes in both mean and variability of the weather variables. All models predicted adverse effects of climate change and resulted in the same ranking of mean climate change scenarios. However, models differed in their absolute values of population viability measures, underlining the need to explicitly choose the most appropriate model formulation and avoid arbitrary usage of environmental drivers in a model. We conclude that further applications of pattern-oriented modeling to butterfly and other species are likely to help in identifying the key factors impacting the viability of certain taxa, which, ultimately, will aid and speed up informed management decisions for endangered species under climate change.

Railsback, S. F. and M. D. Johnson. 2011. Pattern-oriented modeling of bird foraging and pest control in coffee farms. *Ecological Modelling* 222:3305-3319.

We develop a model of how land use and habitat diversity affect migratory bird populations and their ability to suppress an insect pest on Jamaican coffee farms. Bird foraging—choosing which habitat patch and prey to use as prey abundance changes over space and time—is the key process driving this system. Following the “pattern-oriented” modeling strategy, we identified nine observed patterns that characterize the real system’s dynamics. The model was designed so that these patterns could potentially emerge from it. The resulting model is individual-based, has fine spatial and temporal resolutions, represents very simply the supply of the pest insect and other arthropod food in six habitat types, and includes foraging habitat selection as the only adaptive behavior of birds. Although there is an extensive heritage of bird foraging theory in ecology, most of it addresses only the individual level and is too simple for our context. We used pattern-oriented modeling to develop and test foraging theory for this across-scale problem: rules for individual bird foraging that cause the model to reproduce a variety of patterns observed at the system level. Four alternative foraging theories were contrasted by how well they caused the model to reproduce the nine characteristic patterns. Four of these patterns were clearly reproduced with the “null” theory that birds select habitat randomly. A version of classical theory in which birds stay in a patch until food is depleted to some threshold caused the model to reproduce five patterns; this theory caused lower, not higher, use of habitat experiencing an outbreak of prey insects. Assuming that birds select the nearby patch providing highest intake rate caused the model to reproduce all but one pattern, whereas assuming birds select the highest-intake patch over a large radius produced an unrealistic distribution of movement distances. The pattern reproduced under none of the theories, a negative relation between bird density and distance to trees, appears to result from a process not in the model: birds return to trees at night to roost. We

conclude that a foraging model for small insectivorous birds in diverse habitat should assume birds can sense higher food supply but over short, not long, distances.

Ruxton, G. D. and G. Beauchamp. 2008. The application of genetic algorithms in behavioural ecology, illustrated with a model of anti-predator vigilance. *Journal of Theoretical Biology* 250:435-448.

We develop a genetic algorithm (GA) approach to a well-known model of vigilance behaviour in a group of animals. We first demonstrate that the GA approach can provide a good match to analytic solutions to the original model. We demonstrate that a GA can be used to find the evolutionarily stable strategies in a model relevant to behavioural ecology where the fitness of each strategy is determined by the frequencies of different strategies in the population. We argue that the GA implementation demonstrates the combination of assumptions used to generate analytic solution to the original model can only be simultaneously satisfied under relatively restrictive conditions on the ecology of the species involved; specifically that group membership is very fluid but group size is conserved over timescales of individual foraging bouts. We further explore the sensitivity of model predictions to alternative choices in the implementation of the GA, and present advice for implementation and presentation of similar models. In particular, we emphasise the need for care in measuring the predictions of such models, so as to capture the intrinsic behaviour of the system and not the remnant of often arbitrarily chosen initial conditions. We also emphasise the potential for GA models to be more transparent about model assumptions regarding underlying biology than analytic models.

Schmolke, A. 2009. Benefits of dispersed central-place foraging: an individual-based model of a polydomous ant colony. *American Naturalist* 173:772-778.

Colonies of many ant species are not confined to a single nest but inhabit several dispersed nests, a colony organization referred to as polydomy. The benefits of polydomy are not well understood. It has been proposed that increased foraging efficiency promotes polydomy. In a spatially explicit individual-based model, I compare the foraging success of monodomous and polydomous colonies in environments with varying food distributions. Multiple nests increased the colony's foraging success if food sources were randomly scattered in the environment. Monodomous and polydomous colonies did not differ in foraging success if food sources were clustered in one or three locations. These results support the hypothesis that foraging success serves as a driver for polydomous colony organization. Because transport may occur between the dispersed nests of a polydomous colony, I tested the efficiency of a simple mechanism of food exchange between nests. This mechanism, as introduced previously in the literature, proves insufficient to equalize the level of food between nests. While the importance of transport between nests remains unclear, the model results indicate that polydomy may increase the foraging success of ant colonies and that this effect may be robust across a range of food distributions.

Wang, M. and V. Grimm. 2007. Home range dynamics and population regulation: an individual-based model of the common shrew *Sorex araneus*. *Ecological Modelling* 205:397-409.

Many territorial animals show marked home range dynamics. Depending on food resources and the presence of other individuals, the size, shape and location of home ranges can change even on short time scales. Home range dynamics are thus likely to be an important aspect of population regulation. Most existing models, however, assume static home ranges. We therefore present an individual-based model that describes home range dynamics on a daily time scale. As an example organism, we focus on the common shrew (*Sorex araneus*), which shows a marked territorial behaviour. The proximate purpose of the model is to capture the relation between home range dynamics and population dynamics. The ultimate purpose is to develop a model that can be used for predicting effects of changes in agricultural practice and pesticide risk assessment. In the model, home ranges are represented by a number of cells in a landscape which are used by a particular individual. They are constantly adapted in order to provide sufficient food resources for an animal. When home ranges do not provide sufficient resources, animals disperse. The model is able to reproduce site fidelity of individuals, habitat preference, and dispersal. Population densities in a mixed

habitat structure resulted in densities approximately equal to those reported from field studies. It is shown that home range size and dispersal are density-dependent and therefore likely to have a strong effect on regulation. We conclude (1) that the basic design of our model is also applicable for other species showing a marked home range behaviour, and (2) that a realistic representation of population regulation might require explicit modelling of home range behaviour.

Willis, J. 2008. Simulation model of universal law of school size distribution applied to southern bluefin tuna (*Thunnus maccoyii*) in the Great Australian Bight. *Ecological Modelling* 213:33-44.

A universal law of animal group size distribution correlates well to observed fish school size distribution from fisheries catch data. I applied the law to fisheries independent aerial survey data of southern bluefin tuna (*Thunnus maccoyii*) collected over a 10-year period in the Great Australian Bight. The law does not correlate to the observed school size distribution. A computer model originally demonstrated the formation of the universal law from simple rules. I redesigned this model as an individual-based simulation model calibrated from acoustic tag observations and state a mathematical formula for a resultant new family of transient group size distributions. The new formula correlates accurately to the simulation and to the aerial survey data. I use the mathematical model to estimate area of aggregation and total abundance. This approach is new as it does not seek stationary states of group size distribution and because it demonstrates a quantitative relationship between individual behaviour and group size distribution. This work elevates the pattern of group size distribution from a curiosity to a useful tool, and introduces a new family of transient distributions that may have a general application to other grouping phenomena.

Wolf, M. and J. M. McNamara. 2012. On the evolution of personalities via frequency-dependent selection. *The American Naturalist* 179:679-692. (ODD is in Appendix 2)

Personality differences can be found in a wide range of species across the animal kingdom, but why natural selection gave rise to such differences remains an open question. Frequency-dependent selection is a potent mechanism explaining variation; it does not explain, however, the other two key features associated with personalities, consistency and correlations. Using the hawk-dove game and a frequency-dependent foraging game as examples, we here show that this changes fundamentally whenever one takes into account the physiological architecture underlying behavior (e.g., metabolism). We find that the inclusion of physiology changes the evolutionary predictions concerning consistency and correlations: while selection gives rise to inconsistent individuals and stochastically fluctuating behavioral correlations in scenarios that neglect physiology, we find high levels of behavioral consistency and tight and stable trait correlations in scenarios that incorporate physiology. The coevolution of behavioral and physiological traits also gives rise to adaptive physiological differences that are systematically associated with behavioral differences. As well as providing a framework for understanding behavioral consistency and behavioral correlations, our work thus also provides an explanation for systematic physiological differences within populations, a phenomenon that appears to exist in a wide range of species but that, up to now, has been poorly understood.