ODD Protocol

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Purpose
The study focuses on the effects of a management control on agent population levels. Various degrees of control implementation are evaluated order to investigate the tradeoffs between the effectiveness and number of controls required to maintain low agent population levels. Further, optimal agent dispersal rates for a particular control combination can also be determined.

This model was modified from a model by Poethke *et al.* investigating the emergence of optimum dispersal rates for local extinction events (2003). Poethke observed the evolution of stable agent dispersal rates for density-independent environmental catastrophes and density-dependent environmental fluctuations in population size.

State Variables and Scales
The model involves individual and population level hierarchies for both agents and the patch environment. Individual agents are characterized by age, sex, affiliation with a patch i, and four alleles at different loci p_c (density dependent) and p_k (patch-size dependent) which contribute to dispersal probability (d). Further, once mating with a male, females may produce Λ offspring, Λ being a Poisson-distributed number with a patch and time specific mean, Λ_{mean}(t,patch). Lambda is restricted by the patch carrying capacity. The number of agents on a patch plus offspring will never be greater than that patch's carrying capacity. Offspring develop into mature individuals with a density dependent survival probability s.

All agents are universally affected by dispersal mortality (μ), an agent control mechanism, offspring mortality, and reproductive mutation rate. The mean offspring production of the population is given by *avg-offspring*.

Patches are divided into n_{patch} habitats, each with its own carrying capacity (K_i), agent population size (N_i), and population density (C_i). The average carrying capacity of all patches is $K_{mean} = 100$.

Process Overview and Scheduling
The model progresses in single time steps. For each the following processes occur in order: management control (if applicable), agent aging, agent death (age = 4), dispersal, dispersal mortality, reproduction, and offspring mortality. At each timestep, dispersal probability, offspring mortality, and patch population size fluctuate in accordance with agent death via control, age, dispersal, and reproduction. Management control is determined by the user to occur after a specific number of ticks, when agent populations exceed a set number, or a combination of the two.

Design Concepts
Emergence The model exhibits an emergent stable dispersal rate over the course of a run.

Adaptation Agents with the optimum dispersal rate for a given management control combination will survive longer and produce more offspring than non-optimum agents. As their genes dominate the gene pool, the overall population will gradually adapt to a given control mechanism.

Fitness Fitness is determined by agents surviving longer (e.g. avoiding population control) and producing more offspring. Agents having an optimum dispersal rate for the particular control technique will have a higher fitness.

Sensing Individuals are assumed to know their own age, sex, and density, and apply those values to dispersal probability, dispersal, reproduction, and offspring survival probability.

Interaction Two forms of interaction are modeled: direct interaction via male-female reproduction, and indirect through density-dependent variables (e.g. dispersal probability).

Observation Trends in population levels and dispersal rate are constantly monitored throughout the experiment, with the final dispersal rate, average, mean, median, and min/max population levels being recorded at the end of the 1,000 timestep limit.

Initialization
At initialization, each patch i is assigned a K_i taken from the uniform distribution $10 \leq K_i \leq 190$ such that $K_{mean} = 100$. Individual agents are given an age, sex, and a patch affiliation as well as allele values of p_c =1 and p_k = 0. Surviving offspring at each timestep are reassigned p_c and p_k values according to the mean allele values of their parents or mutation.

Simulations are run under two methods of management control:

- *Time Control* All populations face an externally determined extinction risk independent of patch population or capacity. Populations will be randomly destroyed every a give period (*control-interval*) and intensity (*control-amt*).
- *Pest Number Control* Like the time control regiment, populations are subject to random extinctions according to overall agent population numbers. Agent threshold is determined by the user via *pest-thrsh*. If population numbers exceed the threshold a predetermined control of *control-amt* patches will be implemented on the patch environment.

In both scenarios, dispersal mortality and mutation rate were set to 0.10 with an initial agent number of 300 and average offspring (*avg-offspring*) of 10. Control intensity, the number of patches affected by a control regiment (*control-amt*), was defaulted to 15.

Input
For each timestep Λ_{mean} (t,patch) is drawn from the logarithmic distribution with a user-defined mean offspring (*avg-offspring*). However, the number of individuals on a given patch plus their offspring is limited to the carrying capacity of the particular patch.

Submodels
Dispersal
At each time step, mature individuals (age two and above) disperse in proportion to their individual dispersal probabilities, *d*. *d* is determined by

local patch size and density given by:

$$d = \begin{cases} 0 & \text{if } C_i \leq C_{th} \text{ or } C_i = 0 \\ 1 - \frac{1}{C_i}(p_c - \frac{p_k}{k_i}) & \text{if } C_i > C_{th} \end{cases}$$

C_i - population density in patch i
$k_i = \frac{K_i}{K_{mean}}$ - relative carrying capacity of patch i
$C_{th} = p_c$ - $\frac{p_k}{k_i}$ - patch size dependent threshold density

Dispersal is a density dependent factor. In patches with higher densities, agents will be more likely to disperse: p_c and p_k (the genetic component) combined with a low patch carrying capacity will lead to a smaller patch size dependent threshold density. Dispersal is also assumed to be global. That is, an agent has the potential to reach any patch except its own with the same probability: $\frac{1}{(number of patches)-1}$

Reproduction
Once a female interacts with a male, both ages two or above, it is able to produce ε offspring. Each offspring is assigned an age of zero and p_c and p_k values that are the mean allele values of the parents. However, there is a probability of mutation, leading to the evolution of density and patch-size dependent dispersal strategies.

Offspring Mortality
Before offspring develop into mature adults, there is an initial density dependent probability of mortality (s) given by the equation:

$s = \frac{N_i}{K_i}$

N_i - populations size in patch i
K_i - carrying capacity in patch i

Like dispersal probability, offspring mortality is density dependent. At higher patch population sizes and lower patch carrying capacities, there is a much greater chance that an offspring will not survive.

REFERENCES

Poethke, H. J., Hovestadt, T., Mitesser, O. 2003. Local Extinction and the Evolution of Dispersal Rates: Causes and Correlations. The American Naturalist 161(4)631-640.