Individual-based population models: Linking behavioral and physiological information at the individual level to population dynamics[1]

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Abstract. *The development of individual-based computer simulation models of populations and communities provides a means for including large amounts of behavioral information in population and community models, something that traditional models can not do. Individual-based models earl project the affects of organism behavior to the community level. The advantages of this approach have been exploited in many problems; competition for or occupation of space, transmission of diseases or disturbances across populations, movement and feeding patterns and their effects at the population level, and heterogeneous demographic characteristics. Examples of these model types are described. The role of individual-based modeling both in the scientific study of the population-level consequences of behavior and in addressing applied ecological problems is discussed.*

Introduction

In his book, *Sociobiology,* Edward Wilson envisioned the rapid expansion during the last decades of the interface between "sociobiology, behavioral ecology" on the one hand, and "population biology" on the other hand. There are two aspects of this interface. The aspect most interesting to Wilson and other sociobiologists is how population growth, age and genetic structure, and tile environmental forces acting on populations influence the social structure and behavioral characteristics of a species. The other aspect, more interesting to population ecologists, is how the social structure and behaviors of a species might influence the dynamics of the population under various circumstances.

Until fairly recently, population modeling had provided little in the way of tools to help tighten the interface between behavior and population dynamics. In fact, the mathematical models that have predominated in population ecology can represent behavior in only the most abstract collective sense. These models, elaborations on the Lotka-Volterra equations, treat an animal and plant population as variables that can grow or shrink as a function of population sizes of other species. No individual interactions occur in such models.

Nonetheless, during the past twenty years in particular, there has been a trend towards greater detail in population models; particularly in the inclusion of age structure within a population and spatial heterogeneity of the environment. We can make a list of general model types, from simplest to most complex (Table 1). The simplest models contain only one state variable, representing total population size. More complex models have more state variables, representing such things as age and size classes within population and the densities of subpopulations of a spatially distributed metapopulation.

Even the simplest traditional state variable models can contain some aspects of behavior. For example, consider the positive influence of population density on survival and reproduction at low

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population densities that is referred to as the Allee effect. A simple model of a single population in which the Allee effect occurs has the form of the first order differential equation,

$$\frac{dN}{dt} = r(N - N_c)(1 - \frac{N}{K})$$

where N_c is a threshold below which the population is too small for reproduction or other social functions to occur. Behavior in an abstract sense is also incorporated in models of predator-prey dynamics. In demographic analyses of predation, behavior is indirectly incorporated into models in feeding functions termed functional responses. For example, when a consumer seeks out prey it spends time searching and handling prey. Its ability to locate prey may depend on a search function. In this case we can derive functional responses, F(N), like

$$F(N) = \frac{Crp_0 N^2}{1 + t_h Crp_0 N^2}$$

where N is prey density, r is the encounter rate with prey, C the capture probability, t_h the handling time for a prey individual, and p_0 the coefficient of how the probability of discovering the prey increases with prey density (search-image hypothesis).

Table l. Types of models used in ecology and the variables associated with these models

Model Type	Variables
Population level models	Total population size: $N(t)$ or N_t
Age-structure matrix models	Age-class sizes: $N_{1,t}$, $N_{2,t}$, …

Partial differential equations
  McKendrick - von Foerster
  Sinko - Streifer
	Distribution of ages: $f(a,t)$
	Distribution of sizes: $f(s,t)$

Spatial metapopulation	Populations on spatial patches: $N_1(t)$, $N_2(t)$, …
Individual-based models	Attributes of each individual, i: size, age, spatial location, dominance, aggressiveness, etc.

More details of a behavioral nature can be included by going to age structure models. In these models, the different age classes call exercise different resource choices and different probabilities of reproduction, for example. Space can be included to allow different fractions of a population to occupy different spatial habitats. However, these models still aggregate individuals into classes, as critics have pointed out, which limits inclusion of individual variability and the variability of local population density in space. Lomnicki (1980) emphasized that "Individual differences among population members can have a large influence on overall population dynamics… ". Pielou (1981) listed a number of questions that should be addressed, but that are ignored in aggregated models: "How large, in numbers and area, are fully mixed, completely interacting subpopulations: How widely spaced are they? What is the rate of transdispersal between them? Does transdispersal take place all the time, or seasonally? Do hospitable patches persist, or are they ephemeral?… What proportion of habitable patches are occupied at any one time`? Do the subpopulations exhibit geographic variation in their demographic parameters?" These critics, and others, feel that overly abstract models have widened the gap between theoretical ecology and field ecologists, who are continually made aware of the great complexity that models ignore.

It is a matter of great interest, then, that the rapid increase in the speed and memory of

computers is making it feasible to avoid the assumptions of uniformity and complete mixing in population models and to use simulation approaches compatible with the field ecologists' knowledge of the microscale. Computer simulation models need not lump individuals into abstract variables because they can follow the course of individuals in a population, each with its own physiological and behavioral characteristics. These characteristics of each individual are the variables in the individual-based model, in which sense they are qualitatively different from the other models listed in Table 1, in which population numbers within particular classes within a population are the variables.

The "individual-based" modeling approach is not new. It has been used for more than two decades for studying epidemics, population genetics, and animal movement. Perhaps most of the models have been applied to simulating the activities of individual organisms. However, the relationship between behavior and population dynamics requires that one consider the interactions of many individuals. Our interest here will be only in those models in which a number of individuals are modeled simultaneously.

Review of general categories of individual-based models with behavior

At least four different areas of ecology can be identified to which individual-based models incorporating behaviors at the individual level have been applied:
1. Models of competition for or occupation of space;
2. Models of the transmission of disease or disturbances across populations;
3. Models of movement and feeding and the effects on the population;
4. Models that take into account the heterogeneity of demographic characteristics.
We will consider examples of each of these types of models involving behavioral characteristics.

Models of competition for or occupation of space
How individuals distribute themselves among food or other spatially distributed resources has been studied experimentally and theoretically. According to the *ideal free distribution* (Fretwell and Lucas 1970), the individuals should distribute themselves in such a way that each of them achieves the same pay-off. This is a reasonable theoretical expectation. However, the question might be raised: Given that (1) the individuals do not have perfect global information about their environment, (2) movement from one resource patch to another takes time and energy, and (3) individuals differ in their competitive abilities, how closely can the actual spatial distribution of individuals approximate the ideal free distribution? Regelmann (1984) used a simulation model to simulate an actual experiment with six individual sticklebacks and two resource patches (one with twice the food input, water fleas, of the other) to analyze various behavioral rules regarding patch choice. The following assumptions were made in the model:
1. Each individual knows about the existence of two resource patches; that is, in the memory of each individual the two patches have an equal but very low value when a trial starts.
2. Each individual measures only its own feeding success.
3. Each individual has a memory that decreases exponentially with time; that is, more weight is given to recent pay-offs.
4. Each individual calculates the probabilities of visiting the two patches according to the ratio of probabilities which the individual itself has measured before, via its own food intake, and stored in its memory.
5. Three of the individuals were good competitors and three were poor competitors, the latter obtaining less food in a patch.
6. Costs in time in moving from one patch to another could be imposed, during which no food could be obtained.
The results of the simulation showed that after some short time period the model sticklebacks distributed themselves in an approximate ratio of 4:2 between the two types of patches, in agreement with the experimental results. It was interesting that this 4:2 ratio occurred in the model regardless of whether traveling costs were imposed. The details of the simulation model output allowed

Regelmann (1984) to answer more specific questions. First, how was the 4:2 ratio maintained: through continual movement between the patches such that each individual spent twice as much time on the average at the more profitable patch, or through some initial sampling followed by loyalty of the individuals to a particular patch? The model results suggested that the latter was more likely to occur. Second, how did the individuals sort themselves out in a 4:2 ratio, even though they differed in competitive ability? The simulation showed that the competitively dominant individuals were able to estimate the patch values in a shorter time and sorted out in a 2:1 ratio fairly rapidly. The poor competitors took longer to sort out in a 2:1 ratio, because their assessment of the values of the patches could only be established after the dominant competitors had reached a relatively stable equilibrium.

The advantage of using the individual-based simulation model here is that it was able to address questions about the specific mechanisms by which the experimentally observed distribution might have developed. The model suggested that a distribution similar to the ideal free distribution could occur even when the individuals differed in competitive ability and when there were costs in changing from one patch to another.

Models of transmission of disease across a population: Rabies epizootic
Traditionally, mathematical descriptions of epidemics have been aggregated models with a few equations for a few variables, such as Numbers of infected, susceptible, and immune individuals in a population. Such models have little ability to incorporate detailed behavioral information. Since it is known that behaviors must affect rates of transmission, modelers have turned to individual-based modeling to study how the details of behavior may affect the pattern of spread of an epidemic through space.

David et al. (1982) constructed a model for the spread of rabies by foxes. The authors simulated the epizootic over a 600,000 hectare area by dividing a two-dimensional plane into 12,000 equal elements of 50 hectares each. Eco-ethological data were used to assign processes of aging, reproduction, disperal behavior, territory formation, and range overlap of foxes. Information regarding transmission probabilities between individual foxes in the same cells and the effect of rabies on foxes was also built into the model. Among the important behavioral assumptions were:
1. An average fox home range of about 400 hectares.
2. A density of foxes not exceeding eight per 400 hectares.
3. An annual reproductive period.
4. Dispersal of young foxes in the autumn, with an assumed distribution of dispersal distances in the ranges 1-5 km, 5-20 kill, 20-40 km, and 40-60 km. The young foxes can make up to five attempts to establish a territory, with some probability of dying following each failed attempt.
5. The adult foxes can move from cell to cell in their home ranges.
When a population of model foxes was infected with the rabies virus, the simulation predicted the spread of a rabies as a wave. This spread occurred only if the density of foxes exceeded one fox per 160 hectares. In advance of the wave front, the dispersal of young foxes created small pockets of outbreak. The spatial pattern of these pockets depended on details of incubation period of rabies and density of foxes ahead of the front. Behind the front, the population was severely depressed at first, but could recover sufficiently in three years that young dispersing foxes moving back from the front can cause renewed outbreaks. The model made many specific predictions regarding the pattern of rabies infection that could be compared with field data.

Models of movement and feeding: bird movement patterns in a flock
Simulations of individual movements by animals have long been used to study how various movement behaviors (e.g., klinokinesis, orthokinesis, tropotaxis) can deternine an animal's ability to locate and remain near resources or desired habitat (e.g., Rohlf and Davenport 1969, Kitching 1983, Cain 1985). By simulating the movements of many individuals at once, including behavioral interactions, models have also been used to study how various patterns of aggregation develop. Thompson et al. (1974) used this approach to study the survival value of flocking to birds. Bird feeding in the canopy was simulated by representing the canopy by a grid of 3 ft x 3 ft areas, to which various types of spatial distributions of insect prey were assigned. The model birds were allowed to move in this matrix, their

movements being guided by (1) the search for food, (2) the attraction to other, more successful birds, and (3) repulsion from other birds if density was too high. Flying behavior was also permitted for the birds. The model described very well the sort of movements observed in actual flocks of birds. The authors also tested a number of hypotheses with their model, showing, among other things, that flocking did not significantly increase the capture rate of prey, and so it may serve largely as a defensive function against predators on the birds.

Models of movement and feeding: Juvenile planktivorous fish

Different movement strategies may have different consequences for foraging success and hence for population dynamics. Tyler and Rose (in review) constructed an individual-based model of a juvenile, planktivorous fish population in a heterogeneous environment during the summer growing season. This model explored the population dynamics implications of different habitat selection rules used by individuals. The model environment consisted of distinct spatial cells that vary in their food density and predator number. The optimal choice through time of an individual in an environment in which the individual did not affect the environment has been previously analyzed for by the dynamic optimization approach (Mangel and Clark 1988). However, this approach may not work for a population of animals that have large indirect effects on each other through prey exploitation. In Tyler and Rose's model, the individual planktivores begin with identical attributes, but grow, update their estimates of food availability and potential mortality based on their individual experiences. The questions addressed were (1) how does the rule that individuals use affect the number of fish that survive the juvenile life stage, (2) does the rule that individuals use alter the effect of fish density on growth and survivorship, and (3) what rule should individual fish employ to determine when to depart their current cell?

The model structure and assumptions were as follows:

1. There was a 10 x 10 grid of cells, with each cell representing 10,000 m^3 volume.
2. Zooplankton and predators were distributed among cells at the outset of the simulation. Zooplankton were governed by growth equations. Fifty predators were distributed randomly among the cells. Each cell consisted of some open water and some refuge area with no food.
3. Foraging and growth models were assigned to each individual juvenile zooplanktivore. Survival subsequent to the growing season was assumed to depend on individual juveniles reaching a threshold size by the end of the season.
4. Juveniles moved about the environment cells with various rules departing cells designed to maximize individual fitness maximizing energy gain, minimizing daily mortality risk, miminizing the ratio of mortality risk to growth rate). The results of these rules were compared with random departures.

Simulation experiments showed that the movement rules used by individuals could have a significant effect on the population dynamics. Population survival was poorest for the strategy of minimizing predation risk, because the size threshold was not met by most individuals. The density of juveniles did not affect this. At high juvenile densities the random departure rule was more successful than any other strategy, but at lower densities, both maximization of energy gain and minimization of the risk of predation to energy gain were more successful.

Models of movement and feeding. Wading birds in the Everglades

Declines in populations of and reproductive success of wood storks and other wading birds have occurred in the Florida Everglades over the past several decades. These declines have been concurrent with major changes in the Everglades' landscape characteristics. Among the plausible hypotheses that relate to landscape change are the following: (1) General loss of habitat and (2) heavy loss of specific habitat, namely short-hydroperiod wetlands that provide high prey availability early in the breeding season.

These hypotheses were compared using an individual-based model of wading birds (wood storks, *Mycteria americana*) reproduction (Fleming et al., 1994). This model simulated the behavior and energetics of each individual wading bird in a breeding colony on 15-minute intervals. Changes in water depth and prey availability occurred on daily time steps. Simulation results showed a threshold

response in reproductive success to reduction of wetland heterogeneity.

The individual-based model simulated a colony of wood storks for a period of time immediately preceding the formation of a nesting colony and then the whole of the nesting season. This model is described in detail by Wolff (1994), who also gives the sources for all of the assumptions that are built into tile model. In this model each of the adult nesting birds as well as each of the offspring of these adults were modeled as individuals.

The model consisted of tile following parts; (1) a submodel of the heterogeneous landscape, which has water depth as the key variable, (2) a submodel for the prey population, which varies spatially and temporally across the landscape, (3) a set of subtuodels for the behavior and energetics of each potentially nesting adult, and (4) a set of submodels for the energetics and growth of each nestling, until the nestling, is fledged or dies.

The importance of spatial heterogeneity of tile environment surrounding tile colony required that heterogeneity be taken into account, which was done through division of tile potential foraging area into 25,600 contiguous square cells, each 1/4 kin by 1/4 km. Each cell had its own mean elevation. so that the whole set of cells described tile typical topography of the central part of the southern Everglades. As the general water level receded during the dry season, the average water depth in each of the cells went down until either the cell dried out or rainfall from tile new rainy season started raising its level again. Water depth in the spatial cells changed on daily time steps. The prey for the wood storks consisted of small fish and macroinvertebrates. The prey in a given cell were assumed to be available to the wood storks using the cell only when the average water level of tile cell is within a certain range (10 to 40 cm for wood storks).
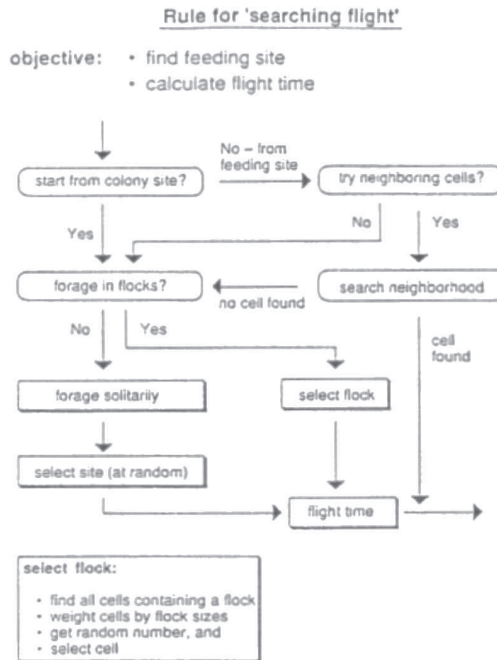
The nesting adult wood storks were described by a set of rules that governed their behaviors from one time interval to the next. For example, Figure 1 shows the choices confronted by a bird in choosing to move in space. The time unit chosen to describe the behaviors of the adult birds was 15 minutes. This time unit was chosen because many discrete activities of wood storks, such as carrying food back to tile nest, take time intervals as short as 15 minutes.

Each adult had to meet a maintenance energy demand each day. To meet this demand tile adult used the first part of the food it collected in a given day for itself. The individual birds usually foraged between 10:00 and 16:00 each day, with each bird deciding when to start and whether to follow others or to go by itself. The location chosen by an individual for foraging was based on its partial information concerning the system. It was assumed that each wood stork had some knowledge, perhaps obtained from visual cues when flying or soaring, concerning the water depth of various locations (cells in the model) in its foraging area. But a wood stork was not assumed to know the prey density in a given cell until it had sampled it for some time (15 minutes). The wood stork could select a cell in the appropriate water depth range, but randomly otherwise, and forage for food in that cell. Alternatively, it could decide to join one of several flocks of birds from the colony that were already feeding. Though each capture of prey by a bird was a stochastic event, the rate of prey captures depended on the current fish density of the cell. Because tile wood stork is a tactile forager, its foraging efficiency should be roughly proportional to the (mean) density of prey within a cell.

If the wood stork found no prey during a 15-minute interval, it moved to another cell, either one nearby or at some distance, although there were greater costs in travel time in flying to a more distant foraging site. Again, it could choose to feed solitarily or join a flock (Figure 1). Probabilities for such choices were assigned in the model. It should be noted that the presence of a flock usually indicated high food density, though it may have been depleted already by the birds foraging there.

The daily growth of the nestlings was computed on the basis of the energetic value of tile daily ration of food brought by their parents. If the nestling did not receive this amount of food before the rainy season begins and adult foraging capability decreases, the model nestling would usually die, because tile parents would no longer be able to provide food at a rate sufficient for its survival. Also, if over any five-day time period during the nesting season a nestling received less than a certain percentage of its cumulative food needs, it died. If tile parents could not find enough food to meet their own energetic demands, they abandoned their nest and tile nestlings perished.

Model experiments were carried out to compare the hypotheses under consideration: "general habitat loss," and "specific habitat loss," (see Fleming et al., 1994). One can also use the model to

Rule for 'searching flight'

objective:
- find feeding site
- calculate flight time

start from colony site? — No – from feeding site → try neighboring cells?

Yes | No | Yes

forage in flocks? ← no cell found — search neighborhood

No | Yes | cell found

forage solitarily | select flock

select site (at random)

flight time

select flock:
- find all cells containing a flock
- weight cells by flock sizes
- get random number, and
- select cell

Figure 1. A schemata showing some of the searching choices that are made by a wading bird in moving from one spatial cell to another.

study the effects of various behavioral characteristics on breeding success.

In an effort to assess the role of adaptive foraging behavior in heterogeneous environments as a factor determining the success of the colony, we used single-colony individual-based models for the Great Blue Heron (*Ardea herodias*) and Wood Stork (*Mycteria americana*). Heavy loss of specific habitat, tamely short hydroperiod peripheral wetlands that provide high prey availability early in the nesting season is examined as a possible source of reproductive failure in the model 50-pair colonies. We assumed that both species could respond to the resource scarcity by using the most profitable foraging mode in each case.

We used two scenarios under which simulations of both models were performed:

Case 1. A breeding season where the extent and location of profitable feeding sites ensured a high food availability in the proximity of the rookery.

Case 2. A breeding season that starts off as in Case 1, but with heavy rainfall events that caused water reversal that disrupted the drydown during the critical last weeks of the Nest disturbance.

Our simulations confirmed that the wood stork is the species most sensitive to variations in the water level, because unlike visually hunting species of herons, the stork feeds exclusively by non-visual, tactile methods and its feeding efficiency is directly related to fish density. In Case 1, the wood stork had a large rate of acquisition of food, because it normally fed in flocks and took advantage of information provided by other wood storks concerrting which feeding sites were good (Figure 2a). However, in Case 2, after the occurrence of rainfall events the wood stork fared much worse than Great Blue Herons (Figure 2b). There were no areas of concentrated prey for flocking to provide information on. The Great Blue Heron required smaller prey density for success, and so was able to maintain relatively high prey intake.
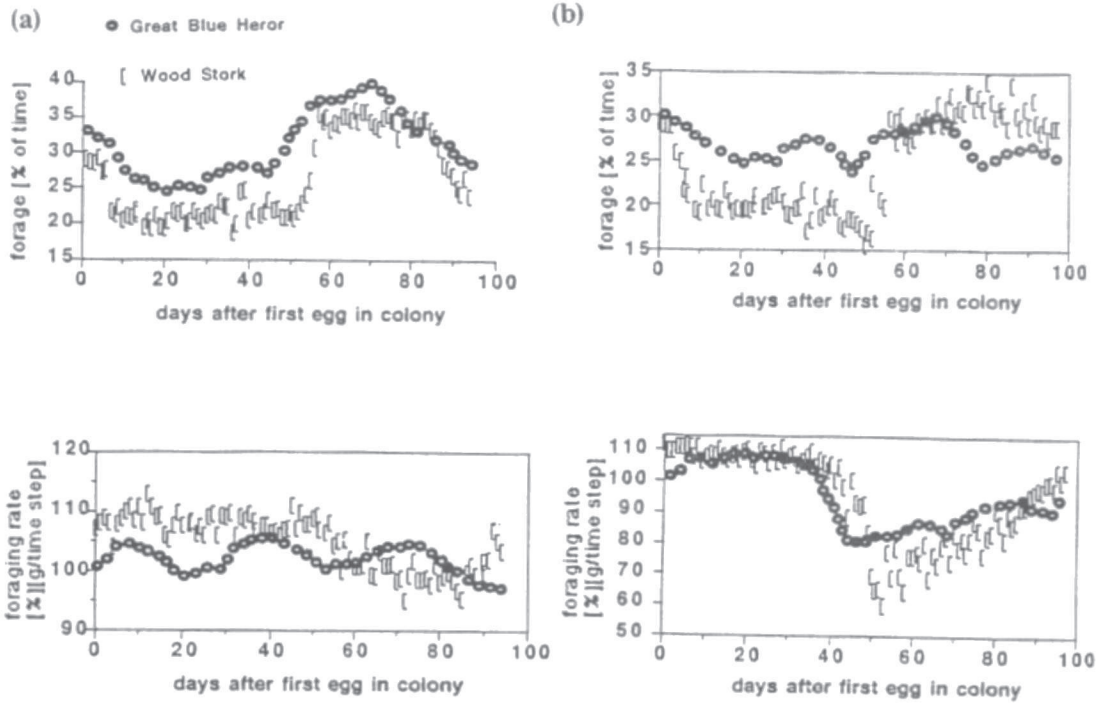
Figure 2. Comparison of the foraging rate, or rate of prey acquisition (grams per 15-minute interval) of two wading bird species (wood storks and Great Blue Herons) over the breeding season: (a) for a dry season without major rainfall events and (b) for a dry season with major rainfall and flooding. Note that in a normal dry season without floods, sodd storks have a higher rate of food intake, whereas in a year with flooding (and reversal in water depth decline), the Great Blue Heron's feeding strategy is superior.

Models that take into account the heterogeneity of *demographic characteristic:*

Local populations and, in some cases, the total populations of species, are frequently small enough that their dynamics, including the possibility of extinction, may depend on stochastic events, such as mortality, at the level of the individual, and may also depend in detail on the age structure, relatedness of individuals, sex ratio, and the distribution of genotypes in the populations. As Lomnicki (1980) has pointed out, individual differences between population members can have a large influence on overall population dynamics and can be a stabilizing factor. Individual-based models are appropriate for such populations.

Among the early attempts at dealing with problems of demographic heterogeneity are models of gene persistence and spatial dynamics in populations. MacCluer (1967) noted that demographic characteristics had seldom been considered in previous population genetics models. Some of these characteristics include the relationship between age and mate choice or genotype and reproductive success. The classical model of random mating is not realistic. MacCluer developed a computer model that iterated over each individual in a deme. It included one locus with up to ten alleles. Details of assortive mating were built into this model.

Schull and Levin (1984) used a similar model to study the genetics of small groups (50-200) of humans in primitive communities. They were able to consider such problems as the effect of discrete overlapping populations on genetic drift. Only one locus and two alleles were modeled. Another problem considered was the maintenance of the balanced polymorphism when there was complete selection against one homozygote and 20 % selection against the other (a case similar to the sickle cell trait). Schull and Levin found that the sickle cell trait should be maintained at the 0.166 level. Levin

(1967) applied a similar model to simulate the Rh locus in humans and the maintenance of Rh polymorphism.

Discussion

The models described in this brief review are only a few of many that have been developed to link individual organism behavior to population and community dynamics. Our aim has not been to be comprehensive but to indicate the main lines of development. Besides dividing these models into the four general ecological categories, we might also classify the models by their intended application. The models described fall into two types; those meant to pose or test scientific hypotheses and those meant to address applied problems of conservation or management.

Both the vulpine rabies model and the wading bird model are of the second type. These models included all behaviors that were felt to be relevant to the issue. In the rabies model this particularly included such factors as the overlap of fox territories and the dispersal of young foxes. Many types of behavior not obviously relevant to the spread of the disease were deliberately ignored. Similarly, in the case of the wading bird model, the important behavioral factors were felt to be those that affected energy intake by the birds, as well as such effects of energy intake as nest initiationand nest abandonment. Other factors, such as the responses to predators were ignored here. This is not because these might not be important, but the practical problem was to assess the consequences of changes in the landscape only on prey acquisition by the wading birds. If changes in the landscape might be suspected of affecting the density of potential predators in a significant way, then it will make sense to change the model to include this and, therefore, to include anti-predator behaviors of the wading birds.

The other models discussed were driven by curiousity in understanding the mechanisms by which individual behaviors lead to population level effects. A simple set of rules was hypothesized and the model was used to project the population patterns that would be produced by these rules. It is noteworthy that the rules used in these models were very simple and could be stated in a few lines. The fact that these rules were assigned to each individual meant that predictions were made both at the individual and population level. The modeler could compare model results with the complex observed patterns of the whole population, but could also single out individuals in the model and compare their behavior with observed individuals. Hence, the capacity for testing ecological theory, both at the behavioral and population levels, is greatly increased in these models.

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