

Young Scientists Summer Program 2006

Four Research Projects

**Evolution and Ecology Program
International Institute for Applied Systems Analysis
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Evolution and synchronization in ecological networks

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Goal

To investigate how evolution affects synchronization in ecological networks.

Background and motivation

Plant and animal populations seldom live in a single homogeneous area, since landscapes are often spatially fragmented into various patches. Migration between different patches may be considerable, especially when patches are not too distant from one another. Such spatially structured populations are described as metapopulations or as ecological networks, where the nodes of the network graph correspond to patches and the graph's arcs to migration flows. Each node may harbor many species and/or various morphs of the same species. If patches have similar geological and climatic characteristics, also the structure of the populations associated with each node are intrinsically similar.

In a great number of ecological networks with highly diversified geographical extent and taxa, changes in the abundances of the same population in different patches are highly correlated over time. This property, often called population synchrony, has been documented with reference to many taxa, including aphids and butterflies (Hanski and Woiwod 1993, Sutcliffe et al. 1996), moths (Myers 1998), fishes (Ranta et al. 1995a), crabs (Higgins et al. 1997), birds (Ranta et al. 1995b, Cattadori et al. 1995a), voles and mice (Ims and Steen 1990, Bjornstad et al. 1999), hares (Ranta et al. 1995a), squirrels (Ranta et al. 1995a, 1997), lynx (Moran 1953, Elton and Nicholson 1942), sheep (Grenfell et al. 1998) and others (Liebhold et al. 2004).

Synchrony may arise from two independent mechanisms: (a) migration (dispersal) of populations among patches and (b) dependence of all population dynamics on some common environmental noise (rainfall, water temperature, etc.). The latter mechanism is known as the Moran effect (Moran 1953). (A third mechanism that has been sometimes been mentioned under the notion of entrained synchrony, is based on trophic interactions with populations of other species that are themselves synchronous. This, however, implies the operation of one of the two aforementioned mechanisms and therefore appears to be of lesser interest.) Both mechanisms are almost always present together, and this has generated a large debate about their relative importance. For example, with regard to Canadian lynx, only a few authors believe that the Moran effect is the main one responsible for synchronization (Sinclair et al. 1993, Cazelles and Stone 2003), particularly after the discovery (Shwartz et al. 2002) of high gene flow across distances of 3000 km. By contrast, for Dungeness crabs, even though pelagic dispersal of larvae has been ascertained, Higgins et al. (1997) showed based on a stage-structured model that the Moran effect may lead to large fluctuations with multi-year cycles that seem to be locked.

Ecological networks with wild but synchronized local dynamics are so ubiquitous worldwide that one is naturally brought to question whether this might be due to Darwinian evolution. Since this question, introduced in (Rinaldi 2006), is at the moment

addressed only indirectly, and only based on empirical evidence, it is of great interest to analyze it from a theoretical perspective.

Research questions

The main purpose of this project is to examine the role of evolution in synchronizing ecological dynamics, by studying various versions of a simple but generic eco-evolutionary model. More precisely, the target is to show that, in the absence of the Moran effect, adaptive traits evolve in such a way that the ecological network tends toward the edge of synchronization. A first step in this direction has already been taken in (Dercole et al. 2006), addressing a particular case.

Methods and work plan

Ecological dynamics

We consider a network with N patches and assume that all local populations are described on the ecological time scale by the same model,

$$\dot{n}(t) = f(n(t), x) \quad (1)$$

where $n(t) = (n_1(t), \dots, n_m(t))^T$ is an m -dimensional vector of population abundances and x is an adaptive trait that can evolve on the evolutionary time scale. Thus, in the presence of migration, the ecological model of the entire network is a set of mN ordinary differential equations,

$$\dot{n}^{(i)}(t) = f(n^{(i)}(t), x) - \sum_{j=1}^N g_{ij} D(x) n^{(j)}(t) \quad (2)$$

where $n^{(i)}$ is the population vector in patch i , the $N \times N$ matrix $G = (g_{ij})$ characterizes the network's topology (specifically, g_{ii} is the number of patches connected with patch i , while g_{ij} for $i \neq j$ is 0 if i and j are not connected and -1 otherwise), and the $m \times m$ matrix $D(x)$ is a diagonal matrix with diagonal elements $D_k(x)$ equal to zero if the k th population does not disperse, and positive otherwise. For example, in the case of two patches ($N = 2$), three populations ($m = 3$), no migration in the first population, constant dispersal D_2 in the second population and with dispersal D_3 in the third population depending upon the adaptive trait x , we have

$$G = \begin{pmatrix} 1 & -1 \\ -1 & 1 \end{pmatrix} \quad \text{and} \quad D(x) = \begin{pmatrix} 0 & 0 & 0 \\ 0 & D_2 & 0 \\ 0 & 0 & D_3(x) \end{pmatrix}. \quad (3)$$

Detecting synchronization

The conditions under which the network synchronizes, i.e., under which complete synchronization (defined by $n^{(i)}(t) = n^{(j)}(t) \forall (i, j, t)$) is stable, are rather complex because they depend on local dynamics (f), dispersal (D), and topology (G). Using the master function approach (Pecora and Carrol 1998), the problem of synchronization can be analyzed by separating the information concerning network topology (G) from the rest. Through the computation of a suitable Lyapunov exponent depending upon f and D , a region S in the space (p, x) , where p is a positive real number, can be determined and the condition of synchronization becomes

$$(\lambda, x) \in S, \quad (4)$$

where λ is the smallest positive eigenvalue of the matrix G . (For example, in case (3), $\lambda = 2$.) If the point (λ, x) lies on the boundary of S , we say that the network is on the edge of synchronization.

Evolutionary dynamics

Assuming that mutations are small and rare we can, in principle, derive the canonical equation of adaptive dynamics, which is of the form

$$\frac{dx}{d\tau} = F(x) \quad (5)$$

and describes changes of the adaptive trait x over evolutionary time τ . Equation (5) has to be derived from the $(m+1)N$ dimensional resident-mutant model obtained by adding to the mN -dimensional model (2) N mutant equations (one for each patch i) characterized by a trait x' very close to x . However, the full analytical derivation of (5) is practically impossible if the resident-mutant model is chaotic. Thus the evolutionary problem will be addressed through repeated simulations of the resident-mutant model for many pairs (x, x') of the resident and mutant traits. Each simulation will reveal whether or not the mutant population x' replaces the resident population x , thus defining, step by step, the evolutionary trajectory in x , and thus also the evolution of the point (λ, x) in the space (p, x) . It will therefore be possible to see whether or not evolution tends toward the edge of synchronization.

Previous work

The first numerical experiment of this kind (Dercole et al. 2006) has shown that starting from ancestral conditions in the set S (i.e., starting from a synchronized network) the evolutionary trajectory reaches the boundary of S and crosses it just before stopping at an evolutionary equilibrium. Conversely, starting from a definitely asynchronous network (i.e., far from S), evolution drives the network toward synchronization and stops at the same evolutionary equilibrium outside the region S . This first experiment has thus indicated that evolution may lead to synchronization.

Similar issues have been addressed in two previous studies, by Holt and McPeck (1996) and by Doebeli and Ruxton (1997), by considering a simple one-dimensional discrete-time model. These studies concluded that dispersal of asynchronous populations always increases up to the edge of synchronization, while, more realistically, if a cost is associated with an increase in dispersal, evolution stops before the edge of synchronization is reached (as shown in (Dercole et al. 2006)). A comparison of our approach with (Doebeli and Ruxton 1997) is more difficult, as those authors considered a model that, although looking simple, has a complex bifurcation structure involving multiple attractors.

Work plan

The work plan for this project is to analyze a number of interesting networks using the method of investigation described above. The ecological model will always describe a tritrophic food chain composed of resource (n_1), consumer (n_2), and predator (n_3). The basic model (as characterized by the function f) will be the Rosenzweig-MacArthur model (Rosenzweig and MacArthur 1963), but variants of interest, like tritrophic food chain models with intraspecific competition among consumers, anti-predator behavior, cooperative behavior among predators, will also be considered. As for the adaptive traits, various assumptions will be made, not excluding the case in which the trait impacts dispersal (as in (Holt and McPeck 1996) and (Parvinen 1999)).

Finally, it will also be checked whether or not evolution's synchronization capacity is influenced by unequal dispersal among the considered populations. Other interesting questions concerning, for example, the role played by network dimension and topology, will be considered if time will be available.

Relevance and link to EEP's research plan

Population synchrony is a classical problem in ecology. Understanding whether, and if so how, evolution drives ecological networks toward synchronization is therefore an important problem that targets a topic in the area of interest of EEP. Apart from providing another fundamental application of adaptive dynamics theory, results from this project might eventually also have implications for biological conservation.

Expected output and publications

The results of this study will hopefully give rise to one or more co-authored publications in international scientific journals.

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An evolutionary model of plant succession

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Goal

To investigate the evolutionary origin of coexisting growth strategies in environments with repeated disturbance.

Background and motivation

While all plants use the common resources of light, water, and nutrients for growth, there is great diversity among species in rates of use and mix of inputs (Westoby 1998). Much of this diversity is thought to reflect the evolutionary diversification of a few key traits in response to frequency-dependent resource competition (Niklas 1997, Westoby et al. 2002). In particular, the evolution of plant height is driven by the need for securing light capture. Taller plants shade shorter plants (but not vice versa), with the asymmetry of this interaction favouring additional expenditure on stems (Givnish 1982, Iwasa et al. 1985). By growing taller than surrounding vegetation, plants thus accrue a significant fitness advantage.

Traditionally, competition for light has been seen to favour evolution of greater height at maturity (reviewed in Falster and Westoby 2003). More general models also describe the evolution of larger adult body sizes if body size confers an asymmetric competitive advantage (Law et al. 1997, Kisdi 1999). However, in environments with frequent disturbance (removal of established individuals by wind, fire, or grazing), selection should also favour the evolution of rapid growth rates and early maturation. Following a disturbance, rapid height growth ensures access to light without requiring a large investment in support structures. Consequently, there may be strong selection for traits that maximise height growth rate, and thereby resource acquisition, in vegetation undergoing frequent disturbance.

Several traits can facilitate rapid height growth. Among species regenerating from seed, these include low leaf mass per area (Reich et al. 1992), low stem tissue density (Enquist et al. 1999), branching patterns emphasising vertical extension (Horn 1971, Pacala et al. 1996), and narrow stem diameters (Falster and Westoby 2005). The same leaf and stem traits that facilitate rapid height growth make fast-growing species inefficient, in the sense that a greater proportion of fixed biomass is lost via respiration, tissue turnover or through mechanical instability leading to mortality (Smith 1976). Low efficiency results in decreased longevity and low shade tolerance (Loehle 1988, Condit et al. 1996), preventing fast-growing species from monopolising environments. Low efficiency should also limit size at maturity (Smith 1976), so that fast-growing species tend both to have shorter asymptotic heights and to be shorter-lived (e.g., Falster and Westoby 2005). The full range of strategies may be found at a single locality. Fast-growing species exploit post-disturbance conditions, but are gradually replaced by slower-growing, progressively taller strategies. This temporal partitioning of access to light, known as succession, is a conspicuous feature of most vegetation types.

Even though ecologists have incorporated successional dynamics into models of vegetation growth (Shugart 1984, Huston and Smith 1987, Pacala et al. 1996, Moorcroft et al. 2001), models accounting for the evolutionary origin of rapid height growth and the diversification of strategies along the successional axis are yet to be developed. Meanwhile, there have been significant advances in techniques used for modelling phenotypic trait evolution under frequency-dependent resource competition (review by Dieckmann 1997). Of particular interest are studies outlining how competition between individuals can promote strategy diversification through evolutionary branching (Geritz et al. 1998, Dieckmann and Doebeli 1999, Kisdi 1999). The aim of this project is to integrate state-of-the-art evolutionary models with models of vegetation dynamics, in order to understand the evolutionary origin of coexisting growth strategies in environments with repeated disturbance.

Research questions

Plants will be considered to differ in two phenotypic traits, (a) a growth trait, indicating higher or lower mass-based growth rates; and (b) a maturation trait, indicating the height at which plants switch from allocation towards growth to production of seeds. The implications for evolutionary dynamics will then be investigated, with the following questions asked.

When strategies are allowed to evolve in one trait only:

1. Is there an evolutionarily singular strategy?
2. Will an initially monomorphic population undergo evolutionary branching?
3. Can multiple strategies coexist in an evolutionarily stable coalition?
4. How does this depend on the values of the other (fixed) traits?

When both traits are allowed to evolve simultaneously:

5. Does this lead to an increase in the number of coexisting branches?
6. Do the dynamics lead to correlated evolutionary divergences (are the height and growth traits correlated across branches?), or is any combination of the two traits possible?

These analyses will then be repeated considering different and additional growth traits, resulting in different and additional trade-offs (as described in the next section). Outcomes will be compared qualitatively:

7. Are all traits correlated, or only some?

Analyses will be carried out for a variety of environmental and spatial configurations. Here I am interested in what features the answers to questions 1-7 depend on:

8. How do environmental parameters, such as disturbance frequency and site productivity, affect evolutionary outcomes?
9. Considering patch connectivity, does a metapopulation structure increase phenotypic diversity compared to a single-patch model? Under what conditions do the results of a metapopulation model converge to those of the single-patch model?

The primary objective during my stay at IIASA is to address questions 1-4. Time permitting, also the remaining questions will be pursued.

Methods and work plan

Evolutionary model

Phenotypic trait evolution will be modeled using the adaptive dynamics framework (Dieckmann and Law 1996, Metz et al. 1996, Geritz et al. 1998). Central to this ap-

proach is the calculation of invasion fitness: the per capita rate of population growth for a given strategy in the environment set by the resident strategies (Metz et al. 1992). If, for a given strategy, invasion fitness is greater than zero then a mutant with this strategy has a chance to invade. Evolution can then be tracked by calculating the invasion fitness of mutant strategies adjacent to the resident. The key question is whether an initially monomorphic population can become dimorphic, which can be assessed using pairwise invasibility plots (Geritz et al. 1998). Analogous techniques are then used to model evolution in a dimorphic populations (Dieckmann and Law 1996, Metz et al. 1996).

Evolution will be considered both within a single patch and within a metapopulation (multiple patches linked by dispersal). For plants growing under repeated disturbance, invasion fitness is given by the cumulative number of mutant seeds produced by a single mutant seed throughout the entire period between disturbances. This number has to be averaged over all possible lengths of such periods in the single-patch model or over all patches of the metapopulation. Several assumptions help simplify calculations (Geritz et al. 1998). The population size of each patch is assumed to be sufficiently large such that mutants experience the local environment as determined by residents, but residents are not significantly affected by the mutant. In addition, evolutionary dynamics are assumed to be slow relative to ecological dynamics. For the metapopulation, the framework of Gyllenberg and Metz (2001) and Metz and Gyllenberg (2001) will be employed. The number of patches is assumed to be large (infinite), with each patch following the same local growth model, but with differences in patch states arising from local catastrophes wiping out a patch's population at different times. These assumptions simplify fitness calculations by removing patch-level stochasticity, a dependence on initial spatial configurations, and the complexities of differential dispersal among patches.

The single-patch model requires an assumption about seed dormancy (related to delayed germination), while the metapopulation model requires an assumption about dispersal rates (related to connectivity between patches). Since many aspects of these two models are formally analogous (in each model, for example, seed output must be weighted with a probability density function for the duration of disturbance-free growth), formal links between the results of single-patch and metapopulation models will be sought.

Local-growth model

The purpose of the local-growth model is to determine the trajectory of growth for a patch containing only individuals expressing the resident strategies, based on the number of resident seeds arriving and on their trait values, and subsequently, for a mutant seed arriving at a given time since the last disturbance occurred. At any moment, the local environment in a patch will be characterised by a single number: the time since last disturbance. We call this the successional state. For each successional state, the local growth model provides vectors describing, first, the rates at which seeds are produced by each resident and, second, the height distribution of each resident.

Space will not be considered explicitly. Within each patch, individuals will be assumed to experience each other equally (mean-field assumption). At a later stage after this summer project, deterministic approximations of spatial processes and patterns occurring within each patch (Dieckmann et al. 2000, Law and Dieckmann 2000) may be used.

The local growth model will be adapted from existing models of vegetation (e.g., Friend 1997, Moorcroft et al. 2001, Woodward and Lomas 2004). While these model the dynamics of plant growth in a simplified manner, they account for the dependencies of production on climate and basic physiology, thereby providing realistic cost-benefit curves.

Traits and trade-offs

Evolution of three growth traits will be considered, each capturing a different type of trade-off thought to be important in structuring vegetation:

1. The first trade-off occurs between leaf mass per area (LMA) and leaf longevity (Wright et al. 2004). High LMA results in greater light capture per unit of biomass, and thus faster height growth, but also in shorter leaf life spans and higher tissue turnover.
2. The second trade-off occurs between wood density and the risk of mortality due to structural instability or attack by pathogens (Moorcroft et al. 2001). Lower density increases the economy of growth at the expense of expected longevity.
3. The third trade-off occurs between vertical growth and the efficiency of light interception, through differences in branching architecture (Niklas 1994). Here a topological branching model (or L-system) can be used to translate mass-based growth rates into predictions about vertical and lateral extension and the distribution of foliage (e.g., Niklas 1994, Prusinkiewicz and Rolland-Lagan 2006).

Schedule

Development of the local growth model will begin during May, prior to arrival at II-ASA. The primary focus in June will be on the development of a simple evolutionary model, with single-trait evolution in a single patch. This will be followed by the development of the full evolutionary model throughout July and pursuit of the research questions as outlined above.

Relevance and link to EEP's research plan

This research continues to extend applications of adaptive dynamics theory to specific ecological systems. There are links with EEP's previous work on adaptive dynamics, adaptive speciation, and on spatially explicit evolutionary models. In the longer term, evolutionary submodels might be incorporated into existing "dynamic vegetation models" used to predict the response of terrestrial biosphere to global change. By highlighting this potential, my project will strengthen the profile of EEP among a broader audience of researchers working in ecology and ecosystem science.

Expected output and publications

This work is intended for publication as a co-authored research article and will also be included in my PhD thesis. Results will be presented at a meeting of the ARC-NZ Research Network for Vegetation Function on "Vegetation Schemes in Earth System Models" in September 2006.

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Influence of local interaction, mating, and dispersal on adaptive speciation in sexual populations

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Goal

To analyze conditions for evolutionary branching in a sexual population influenced by local interactions between individuals.

Background and motivation

Explaining the origin and development of species diversity is one of the greatest challenges in biology. To meet this challenge, it is necessary to achieve a better understanding of speciation processes: Speciation is the process by which one species splits into two or more daughter species, which evolve as distinct lineages.

Studies of speciation classically focus on its geographical context (Mayr 1942, 1963) ranging from allopatry (speciation observed when a population gets divided by a physical barrier; after accumulating genetic differences reproductive incompatibility may be established) to sympatry (reproductive isolation and speciation occur without geographic isolation). In the case of the sympatry, there are two main explanations of speciation: ecological differentiation through natural selection (Schluter 2001) and mating differentiation through sexual selection.

Several studies have suggested that in the presence of gene flow between subpopulations, the adaptive evolution of prezygotic isolation mechanisms such as assortative mating may prevent the creation of organisms with intermediate phenotype and thus enable speciation (Dieckmann and Doebeli 1999; Higashi et al. 1999; Kondrashov and Kondrashov 1999; Doebeli and Dieckmann 2003). Assortativeness is a well-known phenomenon in nature, and organisms with complex behavioral may be more likely to form new species because they choose among potential mating partners. They distinguish members of their own species among potential mating partners on the basis of their size, shape, ornaments, and behavior. Such discriminations can greatly influence which individuals are most successful in producing offspring and may lead to the rapid reinforcement of reproductive isolation between incipient species.

Past research has highlighted the importance of spatial population structure for the eco-evolutionary processes underlying speciation. A recent study of sympatric/parapatric speciation along environmental gradients (Doebeli and Dieckmann 2003) also showed that evolutionary branching occurs more easily in spatially structured populations owing to the presence of local adaptation and competition among individuals with low mobility.

Research questions

In this project I will examine an individual-based model of organisms with sexual reproduction, to investigate features of speciation process under sympatric conditions. For this I will try:

- To establish in general how conditions for evolutionary branching are influenced by the spatial structure of a population, by comparing structured and well-mixed populations.

This goal can be broken down into three more specific steps by looking, in turn, at the effects of local interactions, local mate choice, and local dispersal.

- To investigate the influence of local interactions on evolutionary branching.
The more well-mixed a population, or the larger the distances over which individuals interact, the more phenotypes will participate in the competition affecting any focal individual. How this affects evolutionary branching will be examined.
- To investigate the influence of local mate choice on evolutionary branching
I expect to obtain more favorable conditions for evolutionary branching when individuals prefer to mate with similar partners that are situated close to their own location. Owing to the restriction of gene flow, spatially proximity implies phenotypic proximity.
- To investigate the influence on evolutionary branching of the local dispersal of offspring around parents.
Recently it has been shown that in natural populations non-random dispersal results in genetic differentiation in fitness-related traits (Garant et al 2005; Postma and van Noodwijk 2005). I would like to study whether the movement of offspring by short distances away from their parents could result in the formation of local groups of individuals with similar phenotype and how such pattern formation could influence the dynamics of local competition and, in consequence, evolutionary branching.

Time permitting, a related additional question will be addressed:

- To study the influence of sex structure on evolutionary branching.
Previous models have considered hermaphroditic individuals, so that the question of how sex structure affects the process of evolutionary branching still remains open.

Methods and work plan

Model description

At the first step I will construct an individual-based model, along the lines of the model presented by Doebeli and Dieckmann (2003), to study evolutionary branching in a sexual population. Disruptive selection in this model arises from competition for a distribution of resources.

The model describes hermaphroditic individuals with sexual reproduction. Alternatively, the population could also be considered as containing separate sexes, provided that the spatial and phenotypic distribution of males and females is equal. For investigating the influence of the sex ratio, I plan to extend this model to describe male and female individuals separately.

Phenotypes in each individual are determined by three sets of diallelic diploid loci. The first trait (ecological character) will determine the resource use, the second one (mating trait) will be responsible for the degree of assortative mating, and the third trait (marker trait) will determine an ecologically neutral trait that serves as a mating signal. Individuals are characterized by the rates at which births, deaths, and movements occur.

Reproduction occurs with constant intrinsic rate, but individuals depend on the existence of suitable partners for mating in their local neighborhood. The assortative mating in the model will be based either on the ecological trait or on the neutral marker trait. Individuals with a mating character of 0 mate randomly. Individuals carrying more ‘minus’ than ‘plus’ alleles at the mating loci mate disassortatively, whereas individuals with more ‘plus’ alleles are more likely to mate with individuals with a similar ecological trait or marker trait. Offspring inherit alleles from both of their parents at each locus independently. Random mutations of alleles occur with a given small probability.

Each newborn offspring undergoes an initial movement event from the location of its parent. Individuals die according to local logistic competition. Movement occurs at a constant rate, with individuals changing their location by a random distance drawn from a normal distribution.

The model is defined in continuous time and continuous space, with periodic boundary conditions in a uniform square environment. The resource that individuals compete for has a unimodal (Gaussian) distribution. Algorithmically, the model will be implemented using the minimal process method (Gillespie 1976).

Work plan

Based on this model, I will investigate processes of evolutionary branching by changing the population’s spatial structure from structured to well-mixed. In particular, I will study the influence on evolutionary branching of the distances over which individuals interact, mate, and disperse, as described in more detail above.

June: During this month I plan to construct the model and run preliminary computer simulations to test it.

July: I will then establish how conditions for evolutionary branching are influenced by the spatial structure of a population, by running computer simulations to investigate the influence of local interactions, mate choice, and offspring dispersal. If the previous steps will be completed quickly, I will also study the influence of sex structure on evolutionary branching.

August: The first half of this month will be focused on summarizing the results. During the last two weeks, I will concentrate on preparing a manuscript describing these results.

Relevance and link to EEP’s research plan

The proposed research will extend previous studies of mechanisms underlying, and factors influencing, processes of adaptive speciation carried out by EEP (e.g., Dieckmann and Doebeli 1999; Doebeli and Dieckmann 2003).

Expected output and publications

This work will constitute an important part of my PhD thesis and is destined for publishing as a co-authored article in a research journal.

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Ecology and evolution of female mating preferences under size-selective fishing

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Goal

To develop a model for evaluating the ecological and evolutionary consequences of size-selective fishing in sexually reproducing populations exhibiting female mate preferences.

Background and motivation

Harvesting is increasingly recognized as a major selective force driving the evolution of life history traits (Stokes et al. 1993; Ashley et al. 2003). In particular, accumulating evidence suggests a role for commercial fishing in the evolution of fish populations towards maturation at younger ages and smaller sizes (Grift et al. 2003; Olsen et al. 2004; Olsen et al. 2005). By targeting the largest, oldest, and fastest-growing individuals, fisheries create intense directional selection favoring the survival of smaller, younger, and slower-growing phenotypes (Walsh et al. 2006). Consequently, size and age show truncated distributions towards smaller and younger individuals (Conover and Munch 2002), and proportions of individuals maturing at younger ages and smaller sizes are increasing (Olsen et al. 2004; Olsen et al. 2005). In fish populations, the magnitude and the size-selective nature of fishing mortality (Myers and Hoenig 1997), in conjunction with observations of rapid evolution of life history traits in natural populations (Reznick et al. 1990; Rijnsdorp 1993; Haugen and Vollestad 2001; Reznick and Ghalambor 2005) render this concern particularly important (Munch et al. 2005).

The rapid evolution under fishing-induced selection of traits such as adult size, growth rate, age and size at maturation has been discussed in a number of recent publications (Ratner and Lande 2001; Conover and Munch 2002; Grift et al. 2003; Ernande et al. 2004; Olsen et al. 2004; Olsen et al. 2005). Recent studies have found selective harvesting on large fish to result in indirect changes in additional traits such as fecundity (Walsh et al. 2006) and in traits expressed earlier in life such as larval growth and viability. All these characters are known to influence recruitment success (Berkeley et al. 2004a; Berkeley et al. 2004b; Munch et al. 2005).

Yet, little attention has been paid to the effect of harvesting on patterns of sexual selection, despite the potential impact of sexual selection on population growth rates (Côté 2003) and its importance for conservation biology (Legendre et al. 1999; Wedekind 2002; Côté 2003; Wedekind 2003). Among the variety of explanations for the evolution of female reproductive strategies or inter-sexual selection, the “good-genes” models of sexual selection have gained particular attention. These models are based on the prediction that inter-sexual selection improves the average genetic quality and hence the survival of the progeny (Neff and Pitcher 2005). Increased offspring survival might in particular result from a preference for mates with relatively high heritable viability over those with low heritable viability (Howard and Lively 2004): in such a case, mate preferences are expected to be uniform.

Harvesting inevitably restrains the pool of mates available for female choice. A sufficiently strong reduction in male density might result in an “Allee effect”, through the reduction in mating efficiency at low densities (Stephens and Sutherland 1999) caused by the inability of females to find a suitable mate (Bessa-Gomes et al. 2003). Additionally, selective harvesting might affect female reproductive success by acting on those traits on which inter-sexual selection relies. In particular, selective harvesting on size might directly interfere with female reproductive success because size is a commonly used criterion for mate choice. Female mating preferences for large males can be attributed to superior genes inherited by offspring (Williams 1966; Williams 1975; Beacham and Murray 1988b) and to a variety of direct benefits, such as increased sperm quality and/or quantity and better paternal care (Trivers 1972; Williams 1975; Cote and Hunte 1989). Additionally, differences in growth rates are often interpreted as variations in individual quality (Mangel and Stamps 2001). Examples of female preferences for large-sized males are found in several fish species (Beacham and Murray 1988a; Foote 1989; Blanchfield and Ridgway 1999), including numerous poeciliid species (Basolo 2004) and blenniidae (Cote and Hunte 1989; Neat and Locatello 2002). Other teleosts such as Atlantic cod, *Gadus morhua* (Hutchings et al. 1999; Rakitin et al. 2001) or salmonine fish such as brook trout, *Salvelinus fontinalis* (Blanchfield and Ridgway 1999), sockeye salmon, *Oncorhynchus nerka*, (Hanson and Smith 1967; Foote and Larkin 1988; Blanchfield and Ridgway 1999; Blanchfield et al. 2003), dolly varden, *Salvelinus malma*: (Maekawa et al. 1993) or Japanese char, *Salvelinus leucomaenis* (Maekawa et al. 1994) show a preference for males of similar size (size-assortative mating). Thus, by selectively removing individuals based on their size, fisheries might disrupt female preferences for particular individuals, leading to maladapted female preferences and favoring the evolution of alternative female preferences.

Research questions

The three questions at the core of my research project are as follows:

1. Can the maladaptation of female preferences reduce the yield, stability, or recovery potential of exploited stocks?
2. Should size-selective fishing be expected to cause evolutionary changes in the mating strategies adopted by females?
3. How do trajectories and outcomes of female preference evolution depend on harvesting regimes, natural ecological conditions, life history traits and the initial preference of females?

Methods and work plan

Eco-genetic model

To determine the ecological and evolutionary effects of size-selective fishing on stocks with female mating preferences, I intend to develop an individual-based eco-genetic simulation model. This model will describe an iteroparous species in which mate choice and harvesting are size-dependent.

Individuals will be characterized by their age, size, sex, intrinsic growth rate, and maturation status and females will additionally be characterized by their mate preference. The traits likely to evolve under harvesting will be growth, maturation reaction norms and the female preference, i.e. the decay constant of the exponential distribution describing female preference for males of increasing size (see below), and the mean and standard deviation of the normal distribution describing female preference

for size-assorted males (see below). A quantitative genetic approach will be used to express heritability in the evolving traits. Population dynamics will be based on annual time steps for maturation, reproduction, growth, and mortality.

Growth will be simulated with the bi-phasic somatic growth model (Roff 1983; Lester et al. 2004), which assumes growth to be linear prior to maturation and to follow the von Bertalanffy growth model after maturation. This allows taking into account the cost of reproductive investment at the adult stage. Intrinsic growth rates will be allowed to vary between years and individuals, to account for environmental stochasticity and micro-environmental variation.

Probabilistic maturation reaction norms will be used to describe changes in an individual's maturation status. These reaction norms will be linear and modeled with a constant width and evolving intercept and slope. Maturation reaction norms describe the maturation schedule of a genotype under different growth conditions (Stearns and Koella 1986). The probabilistic extension of this approach (Heino et al. 2002) describes the maturation process based on the probability that individuals of given age and size will mature in the next season. This overcomes the confounding effects of growth and mortality by estimating maturation probabilities conditional on individuals having reached a given age and size (Heino et al. 2002; Olsen et al. 2004; Olsen et al. 2005). While phenotypic plasticity in response to variations in growth only displaces expressed phenotypes along the reaction norm, selection acting on age and size-specific maturation probabilities will shift the reaction norm away from its original position (Haugen 2000; Heino et al. 2002; Olsen et al. 2004; Olsen et al. 2005). Thus, probabilistic maturation reaction norms are an efficient tool for detecting evidence suggestive of fishing-induced evolution.

Preference traits and mating

Size will be used as preference trait. Thus, it will be under sexual selection through female preferences and under natural selection through size-dependent vital rates. Initial female preferences will be of two kinds: (i) preference for overall large males and (ii) preference for size-assorted males. In the first scenario, size will be under directional selection, implying preference to increase with the size of males. The preference trait will therefore follow an exponential distribution. In the second scenario, females will prefer males of similar size. In this case the favored male will not be the same for all females. The strength of the preference will be at its maximum for a male to female size ratio close to one. The preference trait will follow a normal distribution. Considering these two types of female preference will help elucidating the importance of female preference for a stock's ecological and evolutionary responses to size-selective harvesting.

Harvesting regimes

Two different harvesting strategies will be adopted: one corresponding to a management policy prescribing a minimum size limit (i.e., all fish above a given size threshold may be caught) and the second corresponding to a size slot or permissive slot limit (i.e., only individuals within a given size window may be caught).

Work plan

First, I will investigate how structuring populations according to sex and considering different female mating preferences will affect their demographic response to the onset of fishing. Here I will focus on analyzing how this response is influenced by the type and strength of female mating preferences. This first step aims only at revealing

the ecological effects of sex structure and mating preference and will not yet involve an evolutionary perspective.

Second, I will allow female preferences to evolve and evaluate how the outcomes of evolution in mating preferences depend on the ecological conditions characterizing the stock. In particular, I will try to understand how varying the strength of harvesting will affect the evolutionary outcomes of preference evolution, without a focus on evolutionary transients.

Finally, armed with an understanding of the ecological consequences of mating preferences and of the evolutionary outcomes of preference evolution, I will characterize evolutionary transients and allow life-history traits and preference traits to evolve jointly. The predicted pace of evolution in female preference will be particularly important for characterizing these transients: slow preference evolution compared with faster life-history evolution and even faster changes in fishing pressure might result in time lags that cause preferences to be maladaptive under the current conditions.

Relevance and link to EEP's research plan

This project aims to evaluate the ecological and evolutionary effects of size-selective fishing on stocks with mating preferences and is therefore directly linked to EEP's focus on evolutionary fisheries management. Additionally, studying fisheries-induced evolution in sex-structured populations exhibiting female mating preferences is a novel contribution to existing applications of individual-based eco-genetic models.

Expected output and publications

This work will be included as a chapter in my PhD thesis and is intended for publication as a co-authored research article.

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