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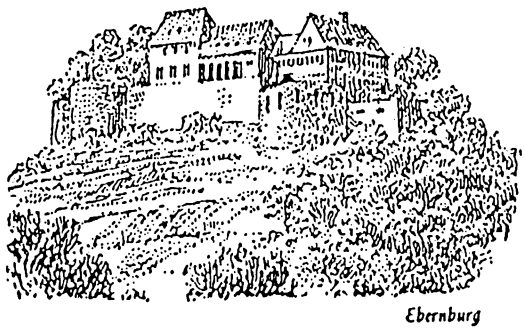

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Predictive Value of Evolutionary Game Theory for Vertical Migration in Zooplankton

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Zusammenfassung. Evolutionäre Spieltheorie ist ein vielversprechender Ansatz, um evolutionäre Aspekte in der Systemanalyse biologischer Prozesse zu berücksichtigen. Anhand der tagesperiodischen Vertikalwanderung von Zooplankton wird beispielhaft dargestellt, wie solch ein Modellansatz zu testbaren Vorhersagen führt. Eine unter speziellen biologischen Randbedingungen durchgeführte Sensitivitätsanalyse erlaubt es, die für dieses Verhalten verantwortlichen Selektionskräfte ihrer Stärke nach zu ordnen.

Summary. To incorporate evolutionary aspects into systems analysis of biological processes, evolutionary game theory is recommended as a promising approach. As an example we present testable predictions on diel vertical migration of zooplankton. A sensitivity analysis performed under constraining biological conditions results in a ranking of different selective forces responsible for this behaviour.

1. Introduction

The coexistence of two similar freshwater zooplankton species with very similar morphology and physiology but different behaviour with respect to diel vertical migration can be explained by a game theoretical model (Thomas and Gabriel 1988, this volume). It is demonstrated that such an approach to a complex system gives insight into its structures and helps to understand underlying evolutionary processes. Here we will show that this model is also of great predictive value and has explanatory potential. Without quantitative and qualitative predictions it would be impossible to design experiments which are able to test whether the basic model assumptions are valid and whether the inherent simplifications are justified. because the debate on the ultimate causes of vertical migration still continues (McLaren 1974, Zaret 1976, Enright 1977, Pearre 1979, Wright et al. 1980, Stich

and Lampert 1981, Weider 1984, Gliwicz 1986, Geller 1987), the model has been formulated quite generally in order to incorporate all relevant forces. The model allows us to rank the relative importance of different factors. We present here a quantified analysis of how diel vertical migration of zooplankton is driven by the interaction of several selective forces.

2. Testable Predictions of the Model

From the model in its general form it follows that the coexistence of different ethotypes, one migrating and the other non-migrating, is evolutionarily stable only under conditions where the algal food of the zooplankton is limited (Gabriel and Thomas 1988a). An observed coexistence of migrating and non-migrating zooplankton would be an unstable situation when food concentration is high. In accordance with this model prediction, there are no observations of such a coexistence in lakes with low algal densities.

The following two questions are important for a deeper understanding of the driving forces in the system:

a) Which predation risk can be tolerated by non-migrating zooplankton?
b) At which threshold value for the efficiency of the conversion of food into successful reproduction does vertical migration to become a favourable strategy?

Model predictions to these questions can be obtained by a proper transformation of the model equations. Gabriel and Thomas (1988b) derived and discussed equations for the maximal tolerable predation risk. If predation risk in the upper water layers during day exceeds the threshold p_{tol}, then vertically migrating ethotypes can invade a population consisting only of non-migrating zooplankton:

$$p_{tol}=(a_d + a_n(1 - \beta_v w/\beta_s))/(a_d(1 + 1.5t_s) + 1.5a_n t_s)$$

with

$$w = (1 + \beta_v a_n t_v) / (1 + \beta_v a_n t_s)^{t_v/t_s}$$

and for $A > A_{lim}$

$$a_d = gA_{lim}(1 - T_n)$$

$$a_n = gA_{lim}T_n$$

and for $A < A_{lim}$

$$a_d = gA[\exp\{(r_p - gx_sN)(1 - T_n)\} - 1]/(r_p - gx_sN)$$

$$a_n = A\exp\{(r_p - gx_sN)(1 - T_n)\}[1 - \exp\{-gNT_n\}]/N \ .$$

A detailed discussion of the parameters is given in Gabriel and Thomas 1988a: x = relative frequency of an ethotype, t = egg development time, A = algal density, A_{lim} = algal density above which the feeding rate of zooplankton is nearly independent of algal concentration, N = population density of zooplankton, p = predation risk for zooplankton by optically orientated predators such as fish in the upper water layers during day, r = partial intrinsic growth rate of algae, T_n = relative length of night (in parts of 24 hours), ß = conversion efficiency of food uptake to successful reproductive output (mortalities other than considered under p are taken into account), g = maximal grazing rate of zooplankton; subscripts n = night d = day s = non-migratory (=stable) and v = migratory strategy.

For the derivations of a threshold conversion efficiency we assume a population consisting only of non-migrating ethotypes and ask for conditions allowing a successful invasion of migrating ethotypes. This is only possible when the payoff for migratting ethotypes is larger than for non-migrating ones. By setting the payoff difference equal to zero (at relative frequency of non-migrating zooplankton arbitrarily close to x_s=1), we get, therefore, a minimal condition for vertical migration. From the payoff equations given by Thomas and Gabriel (1988) we can easily derive

$$(ß_v/ß_s)_{th} = [1 + a_d/a_n - p\{a_d/a_n + 3/2\ t_s(1 + a_d/a_n)\}]/w \ .$$

Vertical migration can never be an ESS for values below this threshold.

From a detailed analysis of $(\beta_v/\beta_s)_{th}$ and p_{tol} we suggested that the reduction of predator-induced mortality is one of the most important selective forces influencing vertical migration and we demonstrated that it is extremely unlikely that metabolic advantages by themselves are the ultimate causes of diel vertical migration in zooplankton (Gabriel and Thomas 1988b and 1988c). But various selective forces interact in a complex way to select for, or against, vertical migration. Relative strength and interaction of single components of these selective forces can be quantified by the following sensitivity analysis.

3. Ranking of Selective Forces

From numerically or analytically calculated derivatives of the payoff difference with respect to the parameters it can easily be studied whether an increase of a parameter value favours the migratory or the non-migratory strategy. The results (see Table 1) are not counterintuitive. The only ambiguous parameter is the length of night; in extreme parameter settings the zooplankton density may cease to favour vertical migration. A sensitivity analysis to quantify the influences of the model parameters is complicated by the high non-linearity of the model equations. One could only perform local analyses at different parameter settings and would have to study all possible combinations of parameter variations. Instead of such a procedure of questionable value we can combine the sensitivity analysis with a biologically relevant question: we look only for the critical situations with equal payoff for both strategies (and only at $A<A_{lim}$) and ask how parameter perturbations change the payoff equilibrium. We performed the following procedure: In a realistic parameter space we randomly chose a combination of parameters. We prove first whether for this parameter set a solution for x_s (the relative density of non-migrating zooplakton) exists with payoff difference zero. This is done by numerically solving the equation

$$0 = (1 - p)\beta_s a_d - 3/2\ p\beta_s(a_n + a_d)t_s + \beta_s a_n - \beta_v a_n w$$

for x_s and by asking whether x_s falls into the interval [0,1] (note that a_d and a_n are functions of x_s as given above). At each such point we then perform a sensitivity analysis by calculating the payoff difference after changing each parameter value separately by 1%. At each parameter setting we calculate the relative sensitivities by weighing the payoff difference for each changed parameter with the sum of absolute values of payoff differences over all parameters. We let this programm run until 1000 parameter settings have been found and calculate mean, median, maximum, minimum and the quartiles. Figure 1 shows the Box-and-Whisker plots of the relative sensitivities. The most sensitive parameters are egg development time and predation risk. These results and especially the ranking order are also quite independent of the parameter space chosen. The calculations for Fig.1 are performed in the following parameter space: A[0.1,0.9], g[0.2,0.9], r[0.1,0.8], N[0.1,1.5], T_n[0.3, 0.7], $ß_s$[7,12], $ß_v$[7,12], t_s[5,15], t_v[10,30], p[0.01,0.4]. In this large parameter space one needs on average 500 trials to find one parameter combination which allows zero payoff difference. (The sucessful combinations are distributed uniformly over each parameter interval, but some parameters may be strongly correlated.)

Table 1 : Selection direction of the model parameters. If an increase of a parameter value is in favour of vertical migration this is indicated by v, in the opposite case by n.

strategy independent parameters:			
A	food concentration (algae density)		n
r	intrinsic growth rate of algae		n
g	maximal filtration rate of zooplankton		n
p	predation risk during day (upper water)	v	
N	density of zooplankton	v	(n)
T_n	length of night	v	n
strategy dependent parameters:			
t_v	egg devel. time of migrating zooplankton		n
t_s	egg devel. time of non-migrating zoopl.	v	
$ß_v$	conversion efficiency of migration z.	v	
$ß_s$	conversion efficiency of non-migration z.		n

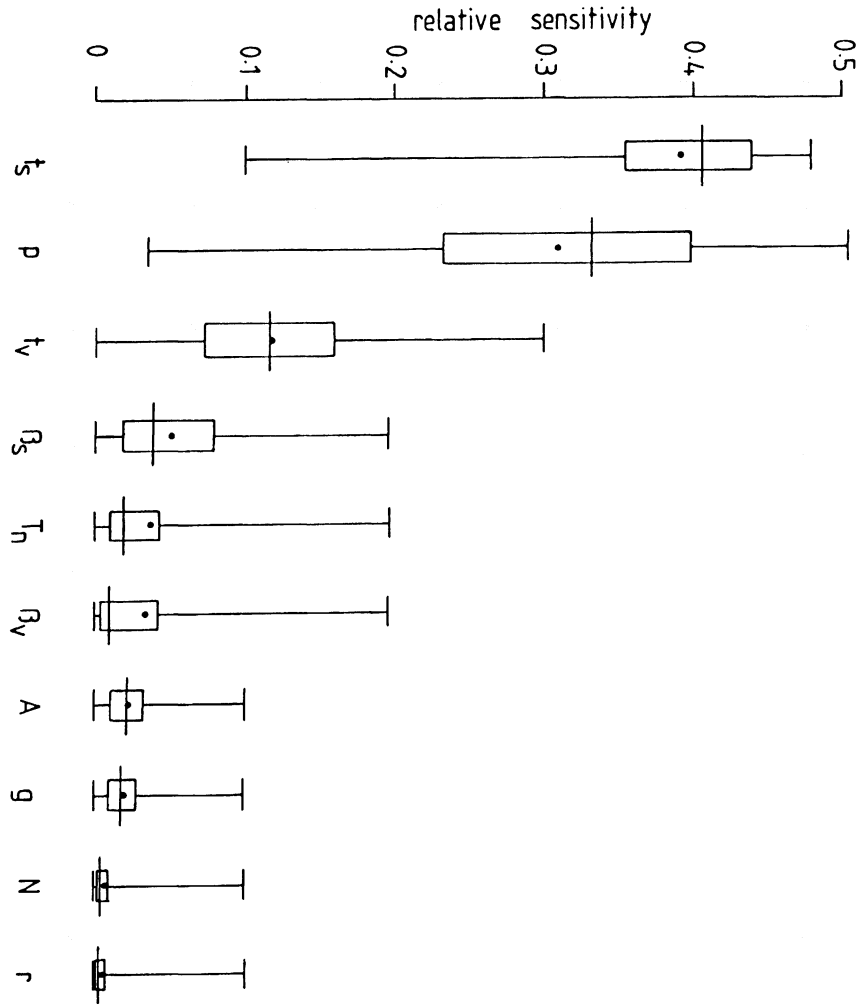

Fig.1 : Relative sensitivity of the model parameters. Mean values are given by points, median values by long horizontal bars. Short horizontal bars indicate maximum and minimum values, the central box covers the middle 50% of the data, between the lower and upper quartiles.

The ranking of parameters gives valuable hints for competition and adaptation experiments, but we have to be cautious with the interpretation of the sensitivity analysis. There may be important adaptational constraints on evolution of special traits, e.g., the most sensitive parameter may be hardest to change or can be negatively correlated to other parameters. The present analysis may hopefully motivate further experiments on vertical migration of zooplankton.

4. Concluding Remarks

A number of problems exist in biology for which the application of tools developed for technical systems is inadaquate or has yet to be extended. Because all biological systems evolve, we cannot ignore evolutionary processes. With our two papers we hopefully demonstrated that a game theoretical approach may be a promising method for the incorporation of the evolutionary aspects into systems analysis of biological processes.

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