Janusz UCHMAŃSKI

Department of General Ecology, Institute of Ecology, Polish Academy of Sciences,
Dziekanów Leśny (near Warsaw), 05–092 Łomianki, Poland

RESOURCE PARTITIONING AMONG UNEQUAL COMPETITORS

ABSTRACT: Intraspecific competition leads to unequal resource partitioning among individuals. Skewness of weight distributions in even-aged populations of plants and animals may be considered as a result of unequal resource partitioning. Properties of the function describing resource partitioning used in the mathematical model of weight differentiation, which simulate all features of weight distributions, are presented. Several experiments which concern relations between competition, resource partitioning and weight distributions are discussed, together with some population consequences of individual inequality.

KEY WORDS: Intraspecific competition, resource partitioning, weight distribution, mathematical model.

1. INTRODUCTION

The term intraspecific competition has a metaphysical meaning in ecology. It is often used as an explanation of ecological phenomena or as a part of interpretations of ecological models. But intraspecific competition alone is seldom the subject of a deeper analysis. In each particular case we are able to replace the word competition by another term or description of the situation (B i r c h 1957, H a r p e r 1977). However, in theoretical considerations it is rather convenient to use this term in its unclear form, with intuitive meaning, which is able to explain everything. In other words, nothing has changed since the time when in 1957 B i r c h discussing various meanings of competition quoted Shelling's statement: "In science as in life men are governed more by words than by clear concepts".

But once such a term exists and seems to play an important role in our image of nature, we should pay more attention to it. There are numerous questions connected with intraspecific competition, partly not solved until now. At first we should be able to present a good definition of intraspecific competition. Next to prove the existence in

real world of the phenomenon defined in this way or at least to present some examples. We should also be able to indicate attributes of intraspecific competition. This is connected with the possibility of distinction between situation when it acts and when it does not. Definitions are general and real world is complicated, so we have to specify mechanisms by which intraspecific competition is working in each interesting ecological situation. And at the end the role of intraspecific competition in ecological theory should be clearly explained.

2. LOGISTIC EQUATION AND YIELD-DENSITY RELATIONSHIPS

What do we know and what can we say about intraspecific competition when we are looking back at the history of ecology. Honestly speaking nothing. Sometimes a decrease of growth rate of a population with increasing density is interpreted as the result of intraspecific competition. In the logistic equation of single population growth, which is of the form

$$\frac{dN}{dt} = rN - \frac{r}{K}N^2 \tag{1}$$

where N is the density of the population, r and K are constants, the second term, proportional to the square of density, often has interpretation directly connected with intraspecific competition. With increasing density environment fills up, the intensity of competition increases and as a result the rate of population growth is reduced.

The logistic equation was often criticized from various points of view. In addition to this discussion one can say that such interpretation as presented earlier says nothing about competition. It doesn't extend our knowledge of competition nor explains why such a form of growth equation should be used, when competition is assumed.

Interpretations of various yield-density relationships and so called $-3/2$ power law for plants have exactly the same value for our purpose. It is well known that yield first increases with the density of plantation, but when some threshold density is passed the yield starts to decrease with further increase in density. Also an increase in plant density N gives a decrease in the mean weight $\bar{w}$ of surviving plants, which often can be described by the following formula

$$\bar{w} \sim N^{-3/2} \tag{2}$$

The interpretations of these observations and formulas include the word competition, but a cognitive value of such statements is practically equal to zero.

Generally it is a common belief that when some characteristic of a population, which is most often calculated as an average over all individuals, depends on density, it indicates that intraspecific competition does operate here. One can consider this as a

definition of competition, but I think that such a definition is not sufficient due to its superficiality.

Of course, our intuition, which is connecting competition with density dependence, probably doesn't lie. Something is going on, what provides such results. However, the empirical facts should be explained not by one magic word, but by some kind of theory.

3. DEFINITION

The need for using such a term as competition rests upon our experience that plants and animals are often limited in space and time. It means that in many situations the available amount of food, energy or other kind of resource when partitioned between present organisms is not sufficient for performing living functions by all individuals. To wait for better conditions is usually a wrong strategy, because the next limitation, that in time, starts to operate. Sufficient conditions of competition include, of course, the assumption that organisms are living together in space. Emigration is not always possible and not always profitable.

But the term competition means something more than living together in space and time with limited resources. Two individuals compete with each other when one of them gains something also needed by the other and what is in limited supply.

This definition implies that the resources, which are the subject of competition game, are not evenly partitioned between competing individuals. Someone is getting more another less. If it is so, it may be the essence of these considerations — an uneven partitioning of resources as the result of competition.

The importance of uneven partitioning of resources between individuals and its consequences were first and often later stressed by Ł o m n i c k i (1978, 1980, 1982). I want only to add that in my opinion uneven resource partitioning as the result of competition is a simple corollary from the assumption that individuals are living together in space and time with limited resources. No sophisticated mathematical models are necessary here.

The definition presented here concerns competition in its strict meaning as used by B i r c h (1957), and an uneven resource partitioning may be the result of both kinds of competition distinguished by N i c h o l s o n (1954): scramble and contest one.

The word intraspecific means that competition takes place between individuals of the same species, for instance, between members of a cohort, for which the conditions of time and space unity are often fulfilled. This last example will be of special interest in this paper.

Let us now look once again at the interpretations of the relationships to density mentioned in Section 2. They are, in the light of what has been stressed in this Section, too vague. The main result of competition — uneven resource partitioning and phenotypic differences between competing individuals as its consequences — cannot be univocally replaced by relationships of average characteristics of population to density.

Relationships between density and various characteristics of population may be of different importance. Some serve as a basis, others are byproducts of the former. These topics should be clarified by analysis of ecological mechanisms working in each particular case.

4. SEARCHING FOR SOLUTION

As far as I know no information based on experiments or observations is available about gains of individual organisms living together and competing for resources. If we limit ourselves to animal bioenergetics we can say that there is no empirical evidence for distribution of resources between particular members of group of competing animals (one known to me exception is discussed in Section 8.2.). Literature data on consumption values and their relation to weight of organisms were obtained from experiments averaging these values over all members of the considered group of animals. The same or even worse situation is in the case of plant ecology. There is no information about the distribution of solar energy or nutrients among individual plants competing with each other.

But the situation is not hopeless. We have no information about gains in resource of an individual and cannot compare them with gains of other competing individuals, but we can trace the fates of particular organisms, which may be more far results of competition, and try to connect them with distribution of resources among individuals.

Almost all organisms are growing. The energy or matter are necessary for growth. So called instantaneous production P of an individual is equal to the difference between the amount A of energy or matter assimilated in the unit time and the total costs R of living in the unit time

$$P = A - R \tag{3}$$

On the other hand, production is the sum of increases in the body weight Δw and instantaneous production of offspring. The actual body weight $w(t)$ of an organism is equal to the sum of increases Δw by the time t

$$w(t) = \sum \Delta w \tag{4}$$

Therefore in nonreproductive periods, for instance, by the time of maturity or between reproductive periods, the weight of an organism is a measure of its net energy or matter gains.

So, on our way of searching for solutions to the problem of intraspecific competition we should analyse the structure of individual weights of the organisms living together and competing for food necessary for living and growth. To clarify the picture, let us limit our attention to even-aged populations. The methods of mathematical modelling may be useful in transforming the description of weight structures in even-aged populations into the analysis of the process of resource partitioning between competing individuals.

Weight is highly correlated with many other features of an individual (P e t e r s 1983). These relationships are not only statistical, but in many cases causal. Therefore the analysis of the weight structure may have a wider ecological meaning.

5. FREQUENCY DISTRIBUTIONS OF WEIGHTS IN PLANTS AND ANIMALS – EXPERIMENTAL DATA

Comprehensive studies on the differentiation and frequency distributions of weights in even-aged plant populations were carried on in Japan in the 1950s. Different plant species were cultivated at variable densities in highly uniform habitats in which plants were evenly spaced. The results of these works were summarized by K o y a m a and K i r a (1956). Similar results were obtained by O b e i d et al. (1967), O g d e n (1970), and W h i t e and H a r p e r (1970). Weight structures of plants under natural conditions were analysed by F o r d and N o w b o u l d (1970, 1971), F o r d (1975) and M o h l e r et al. (1978).

Studies on the frequency distributions of individual weights in animals are very scarce. Most records have been taken on the occasion of the work on another subject. Y a m a g i s h i (1969) and N a k a m u r a and K a s a h a r a (1977a, 1977b, 1977c, 1977d) attempted to analyse systematically the structure of weights and its changes with time, density and food conditions in even-aged fish populations in the manner earlier applied by plant ecologists. The results obtained by these authors are in agreement with results of experiments on plant populations. It is worth to quote also the papers by W i l b u r and C o l l i n s (1973) and C o l l i n s (1979), describing the frequency distributions of weights and their changes with time and density for tadpoles of two frog species.

A more complete list of literature concerning the frequency distributions of body weights for both plants and animals can be found in U c h m a ń s k i (1985). The conclusions may be summarized as follows:

(1) The frequency distributions of individual weights for even-aged plant and animal populations are most often positively skewed.

(2) Symmetric distributions are characteristic of even-aged populations of organisms starting their individual development.

(3) Skewness of weight distributions in even-aged populations varies with individual growth. Two kinds of changes in distribution shapes can be distinguished. In the case of experimental cultures the initially symmetric distributions develop a positive skewness increasing with time. Under natural conditions the same pattern is observed but not exclusively. It also happens that the initially increasing positive skewness begins to decline after reaching a maximum, so that the final frequency distribution can be symmetric again. The decrease of weight distribution skewness is most often correlated with increasing mortality.

(4) The rate at which frequency distributions of individual weights develop increasing positive skewness, and the degree of skewness obtained, largely depend on
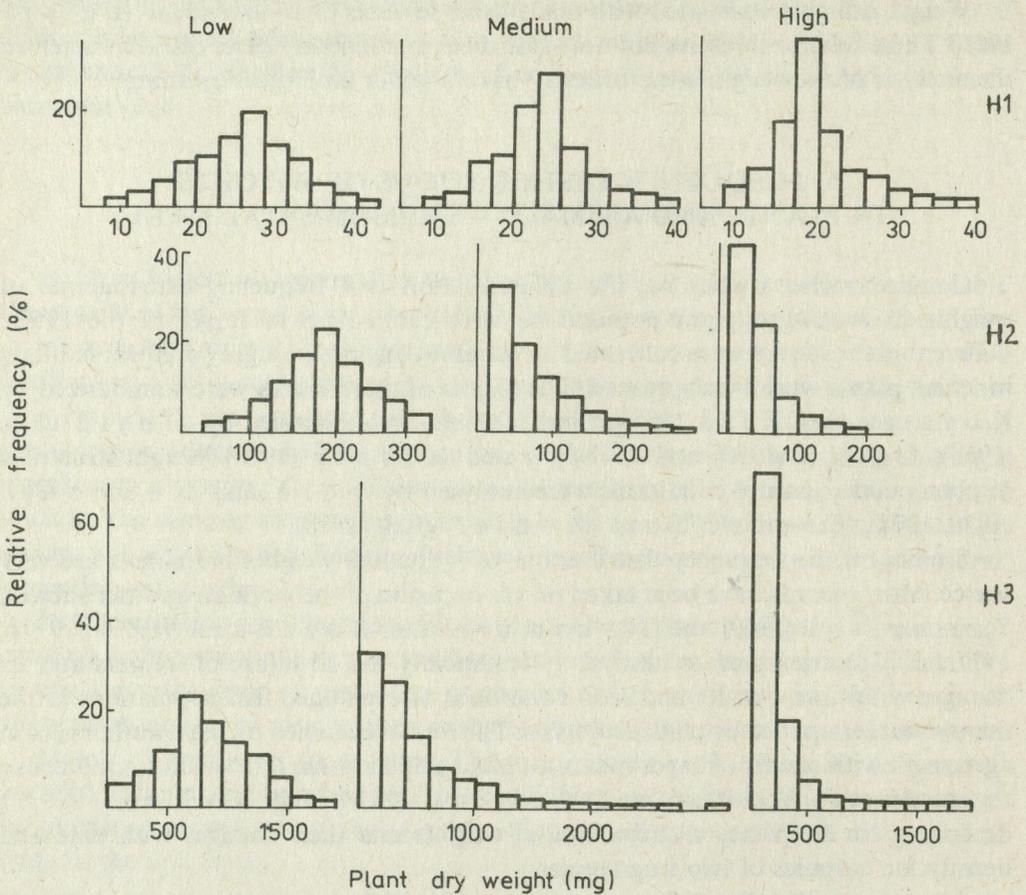
Fig. 1. Frequency distributions of individual plant dry weights in experiments with fiber flax *Linum usitatissimum* L. at three successive harvests (H1, H2, H3) in three densities (low, medium, high) Redrawn from O b e i d et al. (1967)

the population density and environmental conditions such as food quality, concentration and availability. High density and poor trophic conditions enhance the rate of skewness development and increase the value of skewness coefficient (Fig. 1).

(5) Weight variability in even-aged populations measured by the variability coefficient or the variance of weight distribution most often does not follow a regular pattern. But in the case when some regularities are observed, weight variability behaves like skewness. An increase in the density of even-aged population, or a deterioration of food conditions, often account for an increase in weight variability.

However, the picture is not always so clear. A sessile organism, intertidial barnacle *Balanus balanoides*, was investigated by W e t h e y (1983). Only two results are consistent with some events observed in the earlier experiments: the mean size decreased with density and smaller individuals suffered higher mortality than bigger ones. But the rank order of sizes was not strictly conserved during growth. There were

reversals in the size orders. Also the skewness of size distributions positive at the beginning decreased over the growth season. The explanation to this, according to the author, may lay in the fact that the food — suspended particles — for barnacles feeding by filtration may be of different size. Therefore the deterministic process of filtration and random, independent of animal size, events of finding of large particles by small animals should be considered together.

6. THE MODEL

6.1. GENERAL

How to relate the observed·facts to what is going on between individuals? Is it really a result of competition? Let us call mathematical methods for help.

Much depends on the model of individual growth. K o y a m a   and   K i r a (1956) proposed an exponential growth model with randomly varying relative growth rate. They have argued that the observed facts are "the natural outcome of the exponential nature of plant growth as well as variability of relative growth rate, presumably of the Gaussian type", and they need not be the result of interactions among individuals, competition may only exaggerate them. Indeed, they got positively skewed weight distributions, however, they were not be able to explain the changes in skewness with changing density of population and food conditions.

Also other growth models in their classical forms (for review see M a j k o w s k i and   U c h m a ń s k i   1980) are not able to explain the phenomena observed (U c h m a ń s k i   1985). A new description is necessary.

Consumption or assimilation of an isolated individual is a function of the amount of resources available in the environment. In the case of consumption it yields

$$C(t) = C(V(t)) \tag{5}$$

where $C(t)$ and $V(t)$ are respectively: consumption and amount of resources available in the environment, both at time t.

However, for an individual in the group of competing individuals the picture is not so simple because the competition influences the consumption or assimilation of the individual. There are differences between individuals in consumption or assimilation due to competition or, in the other words, resources are not evenly partitioned between competing individuals.

In the case of competition the consumption of an individual still depends on the actual amount of available resources. But it seems to be reasonable to assume that due to competition the consumption of an individual at particular time instant additionally depends on amount of resources consumed by the individual by this time

$$C(t) = C\left(\sum_{\tau = t_o}^{t} C(\tau), \quad V(t) \right) \tag{6}$$

where t_o is an initial time instant.

There are no data on the cumulative consumption of particular individual living in the group of competing individuals. But the weight at time t, as it was stated in Section 4, can serve as a measure of individual cumulative gains. Therefore the equation (6) may be replaced by the following equation

$$C(t) = C(w(t), V(t)) \tag{7}$$

These assumptions about the consumption of an individual in the group of competing individuals may be included into two kind of growth models: deterministic and stochastic one.

6.2. DETERMINISTIC MODEL

It is known from laboratory experiments that under constant food conditions consumption of an isolated individual is in many cases a power function of its weight

$$C(t) = \alpha w(t)^\beta \tag{8}$$

where α and β are constants. Experiments with different food conditions show that consumption of the individual depends on the amount of food available in such a way that only the parameter α varies with food conditions (β is constant).

Because competition is a form of limitation imposed upon the amount of resources available to individual, it seams to be reasonable to assume that in the group of competing individuals differences in individual consumption should be expressed by differences in parameter α.

In deterministic model the future is determined by the past. Therefore the consumption of an individual at time t is determined in the initial time instant. This yields the assumption that the dependence on $w(t)$ in equation (7) as an expression of relation between actual consumption at time t and resources consumed by this time may be replaced by relation to initial weight w_o. Finally, these assumptions and equation (8) give following relationship

$$C(t) = y(w_o, V(t)) \, w(t)^{b1} \tag{9}$$

where b_1 is a constant, $V(t)$ is the amount of food available in the environment and $y(w_o, V)$ is a function describing influences of competition on individual's consumption.

Assimilation $A(t)$ of an individual is often proportional to its consumption

$$A(t) = a_1 C(t) \tag{10}$$

where a_1 is constant coefficient of assimilation efficiency. In addition let us assume that

respiration $R(t)$ is a power function of the body weight and it does not depend on the amount of food consumed

$$R(t) = a_2 w(t)^{b2} \qquad (11)$$

where a_2 and b_2 are constants.

To obtain deterministic growth model it is necessary to substitute equations (9), (10) and (11) into following differential equation

$$\frac{dw(t)}{dt} = A(t) - R(t) \qquad (12)$$

which describes the growth of an individual until maturity or between reproduction periods. This substitution yields

$$\frac{dw(t)}{dt} = a_1 y(w_o, V(t)) w(t)^{b1} - a_2 w(t)^{b2} \qquad (13)$$

6.3. STOCHASTIC MODEL

Let us assume that the environment consists of particles of food. Each particle when consumed increases individual body weight by g. Now the future of an individual is not determined by the past. There is only some probability P of catching a food particle and increasing the weight. We assume that an individual which caught more food particles in the past has a greater probability of catching the next particle than an individual which caught a smaller number of particles. This assumption and equation (6) and (7) give following relationship

$$P = P(w(t), V(t)) \qquad (14)$$

It is possible to make a simplifying assumption that the respiration in a unit time is not related to the success or failure in catching of food in this time, but it depends on the actual weight of an individual according to the power function given by (11). Thus the individual with weight $w(t)$ at time t will have at time $t+1$ weight

$$w(t+1) = w(t) + g - a_2 w(t)^{b2} \qquad (15)$$

with probability $P(w(t), V(t))$ or weight

$$w(t+1) = w(t) - a_2 w(t)^{b2} \qquad (16)$$

with probability $1 - P(w(t), V(t))$ under condition that the amount of food in the environment is equal to $V(t)$.

7. RESULTS

A detailed mathematical analysis of these two models is presented in the paper of U c h m a ń s k i (1985). Here I want to quote only the final results.

Positively skewed weight distributions and desired changes in their shapes with time, density of individuals, and food conditions were obtained in both these models. But the way of resource partitioning between competing members of an even-aged population should fulfil a number of conditions. These conditions concern the dependence of the actual consumption at time t on the amount of resources consumed by the time t, which is represented by the relation of C to $w(t)$ and $V(t)$ (see equation (7)). Each condition for function $C(w, V)$ should be translated into conditions for function $y(w_o, V)$ in the case of the deterministic model (then w is replaced by w_o) and for probability $P(w, V)$ in the case of stochastic model. The conditions are following (an example of the function $C(w, V)$ is shown in Figure 2):
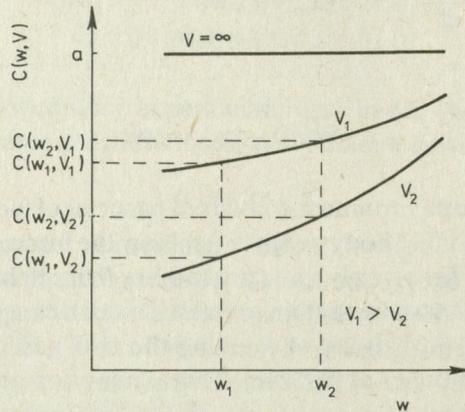

Fig. 2. Theoretical shape of function $C(w, V)$ describing the consumption of an individual living in the group of competing individuals

Assumptions concerning dependence on amount of resource available and weight are illustrated. For explanation of symbols see the text

(1) Under constant food conditions an individual with greater gains in the past gets a greater amount of food in the present. This means:

$$C(w_1, V) < C(w_2, V) \tag{17}$$

where $w_1 < w_2$.

(2) An individual gains more in better food conditions. In other words:

$$C(w, V_1) < C(w, V_2) \tag{18}$$

for $V_1 < V_2$.

(3) Under optimal food conditions food is partitioned uniformly or according to individual's needs:

$$C(w, V)\Big|_{V=\infty} = a \tag{19}$$

where a is a constant.

(4) An improvement in food conditions is followed by a decrease in differences of gains between individuals. It yields:

$$C(w_2, V_2) - C(w_1, V_2) < C(w_2, V_1) - C(w_1, V_1) \tag{20}$$

for $w_1 < w_2$ and $V_1 < V_2$.

(5) A decrease in the amount of food in the environment causes a greater decrease in gains for individuals with smaller gains in the past as compared with those with greater past gains. It is expressed by the formula

$$C(w_1, V_2) - C(w_1, V_1) > C(w_2, V_2) - C(w_2, V_1) \tag{21}$$

for $w_1 < w_2$ and $V_1 < V_2$.

Additionally, the following assumption is also necessary in the deterministic model:

(6) The difference in the amount of food consumed between two individuals of similar gains in the past increases with increasing past gains. This can be expressed by:

$$C(w_2, V) - C(w_1, V) < C(w_4, V) - C(w_3, V) \tag{22}$$

where $w_4 > w_3 > w_2 > w_1$ and $w_2 - w_1 = w_4 - w_3$.

In the case of deterministic model inequality (22) means that $y(w_0, V)$ is a convex function of w_0 for $V = $ const. As the computer simulations have shown (U c h m a ń s k i 1985), the assumption that the probability $P(w, V)$ for $V = $ const. is a convex function of weight much facilitates the development of the positive skewness of weight distributions in the stochastic model.

8. DISCUSSION

8.1. LIMITATIONS OF THE MODELS

The models with the above assumptions were analysed in various configurations (U c h m a ń s k i 1985): a deterministic growth of individuals with constant V, growth of N individuals described by the deterministic model with variable V (constant inflow of food, and food growing according to the exponential law when not consumed), the stochastic model with constant V, and computer simulations of the stochastic model of growth with variable food conditions (the number of food particles given at the beginning was diminished by the number of particles consumed at each time step).

From mathematical point of view these models consist of a set of $N + 1$ equations — N equations describing growth of N individuals and one equation for the description of changes in food conditions V. The right hand side of the last equation is the sum of

two terms. One describing changes in V when food is not exploited, the other, which represents the influence of individuals, is the sum of consumptions over all organisms. Functions $y(w_0, V)$ and $P(w, V)$ do not depend on density of population directly. It means that only competition through exploiting a common pool of food is considered. Interference components of competition among individuals (P a r k 1954), which may depend on density, were neglected.

The general classification of the presented models into deterministic and stochastic corresponds to the classification into plants and animals. The animals, whether carnivores or herbivores in more or less heterogeneous environments, have in many cases only a certain chance of finding food. In this situation the stochastic model is most appropriate. Plants which are competing for light and nutrients can take them in an approximately continuous way — here a deterministic model is relevant. But also animals feeding by filtration are described by this type of model. The best example of organisms described by both type of models are planktonic organisms, including plants and animals.

The fact that models discussed in this paper describe the situation when each individual interacts with all other individuals using the same resource pool inclines us to conclude that in the case of plants the models describe competition for nutrients rather than for light. The competition model for light must consider the spatial structure, that is, the distribution of individuals in space, shape of conopy, the structure of heights, etc. (see models presented by G a t e s (1978, 1982), F o r d and D i g g l e (1981) and W y s z o m i r s k i (1983)).

The example of function $C(w, V)$ presented in Figure 2 describes scramble competition only, because the consumption is greater than zero for all weights. Therefore models discussed in this paper hold when food is in excess or when population density is low, also at moderate food shortages or population densities. They cannot be used for very high densities or severe food shortages. It should be expected that under extremely poor conditions function $C(w, V)$ for constant V will be equal to zero for small weights, while it will take values greater than zero starting from a certain weight. It is also possible that it will be equal to zero over the whole range of weight variability or it will take a constant value close to zero. Such extremal food conditions can produce quite different properties of weight distributions.

8.2. WEIGHT HIERARCHY AND SOCIAL DOMINANCE

The social ranking may agree with the body size ranking, as it was shown in the experiments on rainbow trout, *Salmo gairdneri* Richardson. After initial disturbances, at the end of the experiments the socially dominating individual was also the heaviest one (Y a m a g i s h i 1962).

But not always the picture is so clear. Y a m a g i s h i et al. (1974) described social relations in small laboratory population consisting of four individuals of freshwater eleotrid goby *Odontobutis obscurus* (Temminck et Schlegel). The dominance order was recognized by observing attacking and territorial behaviour of fishes. The

individual food intakes were also measured. The socially dominant fish occupied and defended the all bottom area of the aquarium and together with the second-rank fish surpassed the rest of individuals in the frequency of attacking behaviour. However, the second-rank fish had the greatest food intakes, highest efficiency of food-growth conversion and its weight was greater than weight of the dominant fish at the end of the experiment. Only the weekly variations of food intake were smallest for the dominant fish and they increased with decreasing rank of individuals.

These results show that the social dominance did not agree with the body size hierarchy. Simple bioenergetical model cannot be used here. But, as it is stressed in the paper, an explanation in the language of bioenergetics is still possible. The energy expenditures were greatest for the dominant fish and it was able to devote for consumption only a small part of its activity due to necessity of maintain of dominant social position. The advantage of being the dominant was shown in the experiment with food limitation. The dominant fish was still second in the weight order but its food intakes were greatest in poor food conditions.

8.3. THE ROLE OF COMPETITION

The features of weight distributions in even-aged populations are not exclusively the result of intraspecific competition.

We should take into account the genetic variability in growth of particular individuals. It can be reflected by random variability of the parameters of growth models. It is reasonable to expect positively skewed weight distributions as the result of description of population of isolated individuals by the model with parameters randomly distributed among individuals (K o c h 1966, 1969). For instance, in the early stages of growth, when it follows an exponential curve, random variability with normal type distribution in relative growth rate yields a lognormal distribution of weights (K o y a m a and K i r a 1956).

It is also possible to imagine that a positively skewed weight distribution may be obtained in an experiment with genetically identical individuals growing independently. This is the matter of an appropriate choice of food conditions for particular isolated individuals.

There are few papers describing experiments in which the authors try to indicate differences resulting from treating individuals in isolation and with interactions between them. Recently B r e d e n and K e l l y (1982) reported interesting experiments on toads *Bufo americanus*. Tadpoles were grown in three variants: isolated individuals, one per cup, partially interacting individuals in aquaria with possibility of chemical and visual communication, and fully interacting individuals in open aquaria. Density of tadpoles, food per individual (average values in the case of interacting traits), and experimental treatment were equal in all experiments. Two pairs of adult toads were used to produce tadpoles. In each experiment only offspring of one pair were grown. The authors observed that the variance in the number of days to metamorphosis was smallest in the isolated treatment and fully interacting treatment had the

greatest variance. Also there was a strong positive correlation between the development time and weight at metamorphosis in the interacting treatment, while such correlation did not exist in the isolated treatment. These differences in results for particular treatments are fully explained by the model of influence of intraspecific competition on amphibian metamorphosis presented by W i l b u r and C o l-l i n s (1973).

On the other hand, T u r n e r and R a b i n o w i t z (1983) carried out experiments with the prairie grass *Festuca paradoxa* Desv. Results of these experiments can be interpreted not only as an empirical evidences that competition is not necessary for producing a positively skewed weight distributions, but they can serve as an indication that in some situations interactions between individuals may be an obstacle in development of the positive skewness of weight distributions in even-aged populations. Plants were cultivated as dense cultures or isolated individuals one per container. Distributions of weights of isolated plants skewed first, remained more skewed throughout the experiment, and had a greater skewness than in dense cultures when both distributions were compared at equal mean weights. Additionally, it looks that resource depletion lowering growth rates can decrease skewness of weight distributions, what was manifested in the latest appearance of skewness in nonfertilized cultures.

The explanation of these results proposed by T u r n e r and R a b i n o w i t z (1983) is an extension of the model of K o y a m a and K i r a (1956). Plants grow exponentially with different growth rates. Competition decreases the relative growth rates of all individuals by the same proportion. Therefore the variance of growth rates is reduced and this decreases the variance in individual weights. Recently W e i n e r (1985) and W e i n e r and T h o m a s (1986) are discussing correctness of the above explanation.

8.4. APPLICATIONS

The basic ecological problem, unsolved until now, is why in a given space there is a definite number of individuals, not more or less than observations show. Among various ecological systems, models of which try to answer this question, one is of special importance — a single population. It enables us to investigate intrinsic mechanisms governing the number or density dynamics. However, classical models of single populations are far from reality.

In order to construct more realistic models of single populations one should recall the following basic facts: individuals are born and die, inbetween they reproduce. It is necessary to produce a realistic description of these processes. Like in the description of differentiated growth, we should also include competition into a realistic description of production, survival and mortality of individuals.

Ł o m n i c k i (1978, 1980, 1982) proposes to count all incomes of an individual during one generation and to compare them with some threshold value representing costs of life until reproduction. A positive difference between these values may be

proportional to the production of offspring. An individual dies when its incomes during life are smaller than this threshold value. Unequal partitioning of resources between individuals is necessary for stability of this model of single population.

B e g o n (1984) showed the influence of individual variation caused by the intraspecific competition on dynamics of system of two species. He considered predator-prey dynamics. Prey population with skewed distribution of weights consists of a large number of weak individuals susceptible to predation and a small number of fit individuals able to escape from predation. In such a case, only the individuals of the later group produce the next generation. So the predator population may have only limited influence on the prey population. The same author stressed the role of cannibalism as a regulation factor induced by the size variation of individuals.

9. SUMMARY

The term intraspecific competition cannot be used in ecology in its intuitive meaning. Competition takes place when individuals live together in space and time with limited supply of resources. This implies that resources are not evenly partitioned between individuals.

Reflection of this general fact can be found in patterns of weight distribution in even-aged populations. They are positively skewed and their skewness increases with population density and deteriorating food conditions (Fig. 1).

A relationship between competition and the skewness of weight distribution can be confirmed by mathematical models in which central role is played by a function describing resource partitioning among individuals. Properties of such functions are listed in the paper (Fig. 2).

Not only the intraspecific competition is responsible for skewed weight distributions. One should take into account the genetical variability of growth. The role of competition can be recognized by comparing results of experiments with isolated and interacting individuals.

A nonclassical version of the model of a single population dynamics can be proposed on the basis of the considerations of intraspecific competition.

10. POLISH SUMMARY

Termin konkurencja wewnątrzgatunkowa nie może być używany w ekologii w sposób intuicyjny. Konkurencja zachodzi wtedy, kiedy osobniki żyjące razem w przestrzeni i w czasie natrafiają na ograniczone i niewystarczające zasoby. Wynika z tego, że zasoby te są nierównomiernie jeśli chodzi o potrzeby dzielone między konkurującymi osobnikami.

Odbicie tego faktu można znaleźć w kształtach rozkładów ciężarów w rówieśnych populacjach. Rozkłady te posiadają dodatnią skośność (rys. 1). Ta ostatnia rośnie ze wzrostem zagęszczenia i pogarszaniem się warunków pokarmowych.

Związek między konkurencją i skośnością rozkładów ciężarów może być potwierdzony za pomocą modeli matematycznych, w których główną rolę gra funkcja opisująca podział zasobów między osobnikami. Właściwości takich funkcji zostały przedstawione w pracy (rys. 2).

Nie tylko konkurencja wewnątrzgatunkowa jest przyczyną skośności rozkładów ciężarów. Trzeba także wziąć pod uwagę zmienność genetyczną osobników. Znaczenie konkurencji może być ocenione z pomocą porównywania rezultatów eksperymentów z izolowanymi i oddziałującymi osobnikami.

Na podstawie rozważań dotyczących konkurencji wewnątrzgatunkowej można zaproponować nieklasyczną wersję modelu pojedynczej populacji.

11. REFERENCES

1. B e g o n M. 1984 — Density and individual fitness: asymmetric competition (In: Evolutionary ecology, Ed. B. Shorrocks) — Blackwell Scientific Publications, Oxford — London — Edinburgh — Boston — Palo Alto — Melbourne, 175 — 194.
2. B i r c h L. C. 1957 — The meaning of competition — Am. Nat. 91: 5 — 18.
3. B r e d e n F., K e l l y C. H. 1982 — The effect of conspecific interactions on metamorphosis in *Bufo americanus* — Ecology, 63: 1682 — 1689.
4. C o l l i n s J. P. 1979 — Intrapopulation variation in the body size at metamorphosis and timing of metamorphosis in the bull-frog, *Rana catesbeiana* — Ecology, 60: 738 — 749.
5. F o r d E. D. 1975 — Competition and stand structure in some even-aged plant monocultures — J. Ecol. 63: 311 — 333.
6. F o r d E. D., D i g g l e P. J. 1981 — Competition for light in a plant monoculture modelled as a spatial stochastic process — Ann. Bot. 48: 481 — 500.
7. F o r d E. D., N o w b o u l d P. J. 1970 — Stand structure and dry weight production through the sweet chestnut (*Castanea sativa* Mill.) copice cycle — J. Ecol. 58: 275 — 296.
8. F o r d E. D., N o w b o u l d P. J. 1971 — The leaf conopy of coppiced deciduous woodland. I. Development and structure — J. Ecol. 59: 843 — 862.
9. G a t e s D. J. 1978 — Bimodality in even-aged plant monocultures — J. theor. Biol. 71: 525 — 540.
10. G a t e s D. J. 1982 — Competition and skewness in plantation — J. theor. Biol. 94: 909 — 922.
11. H a r p e r J. L. 1977 — Population biology of plants — Academic Press, London — New York — San Francisco, 892 pp.
12. K o c h A. L. 1966 — The logarithm in biology. I. Mechanisms generating the log-normal distribution exactly — J. theor. Biol. 12: 276 — 290.
13. K o c h A. L. 1969 — The logarithm in biology. II. Distributions simulating the log-normal — J. theor. Biol. 23: 251 — 268.
14. K o y a m a H., K i r a T. 1956 — Intraspecific competition among higher plants. VIII. Frequency distribution of individual plant weight as affected by the interaction between plants — J. Biol. Osaka City Univ. 7: 73 — 94.
15. Ł o m n i c k i A. 1978 — Individual differences between animals and natural regulation of their number — J. anim. Ecol. 47: 461 — 475.
16. Ł o m n i c k i A. 1980 — Regulation of population density due to individual differences and patchy environment — Oikos, 35: 185 — 193.
17. Ł o m n i c k i A. 1982 — Individual heterogeneity and population regulation (In: Current problems in sociobiology, Ed. King's College Sociobiology Group) — Cambridge University Press, Cambridge, 153 — 167.
18. M a j k o w s k i J., U c h m a ń s k i J. 1980 — Theoretical foundations of individual growth equations in animals — Pol. ecol. Stud. 6: 7 — 31.
19. M o h l e r C. L., M a r k s P. L., S p r u g e l D. G. 1978 — Stand structure and allometry of trees during self-thinning of pure stand — J. Ecol. 66: 599 — 614.
20. N a k a m u r a N., K a s a h a r a S. 1977a — A study on the phenomenon of the tobi-koi or shoot carp — I. On the earliest stage at which the shoot carp appears — Bamidgeh, 29: 41 — 44.
21. N a k a m u r a N., K a s a h a r a S. 1977b — A study on the phenomenon of the tobi-koi or shoot carp — II. On the effect of particle size and quantity of the food — Bamidgeh, 29: 44 — 47.
22. N a k a m u r a N., K a s a h a r a S. 1977c — A study on the phenomenon of the tobi-koi or shoot carp — III. On the result of culturing the modal group and the growth of carp fry reared individually — Bamidgeh, 29: 48 — 52.
23. N a k a m u r a N., K a s a h a r a S. 1977d — A study on the phenomenon of the tobi-koi or shoot carp — IV. Effects of adding a small number of larger individuals to the experimental batches of carp fry and of culture density upon the occurrence of shoot carp — Bamidgeh, 29: 53 — 56.

24. Nicholson A. J. 1954 — An outline of the dynamics of animal populations — Aust. J. Zool. 2: 9–65.
25. Obeid M., Machin D., Harper J. L. 1967 — Influence of density on plant to plant variation in fiber flax, *Linum usitatissimum* L. — Crop Sci. 7: 471–473.
26. Ogden J. 1970 — Plant population structure and productivity — Proc. N. Z. ecol. Soc. 17: 1–9.
27. Park T. 1954 — Experimental studies of interspecies competitions. II. Temperature, humidity and competition in two species of *Tribolium* — Physiol. Zool. 27: 177–238.
28. Peters R. H. 1983 — The ecological implications of body size — Cambridge University Press, Cambridge, 329 pp.
29. Turner M. D., Rabinowitz D. 1983 — Factors affecting frequency distributions of plant mass: the absence of dominance and suppression in competing monocultures of *Festuca paradoxa* — Ecology, 64: 469–475.
30. Uchmański J. 1985 — Differentiation and frequency distributions of body weights in plants and animals — Phil. Trans. R. Soc. London, Ser. B, 310: 1–75.
31. Weiner J. 1985 — Size hierarchies in experimental populations of annual plants — Ecology, 66: 743–752.
32. Weiner J., Thomas S. C. 1986 — Size variability and competition in plant monocultures — Oikos, 47: 211–222.
33. Wethey D. S. 1983 — Intrapopulation variation in growth of sessile organisms: natural populations of the intertidial barnacle *Balanus balanoides* — Oikos, 40: 14–23.
34. White J., Harper J. L. 1970 — Correlated changes in plant and number in plant populations — J. Ecol. 58: 467–485.
35. Wilbur H. M., Collins. J. P. 1973 — Ecological aspects of amphibian metamorphosis — Science, N. Y. 182: 1305–1314.
36. Wyszomirski T. 1983 — A simulation model of the growth of competing individuals of a plant population — Ekol. pol. 31: 73–92.
37. Yamagishi H. 1962 — Growth relation in some small experimental populations of rainbow trout fry, *Salmo gairdneri* Richardson, with special reference to social relations among individuals — Jap. J. Ecol. 12: 43–53.
38. Yamagishi H. 1969 — Postembryonal growth and its variability on the three marine fishes with special reference to the mechanism of growth variation in fishes — Res. popul. Ecol. 11: 14–33.
39. Yamagishi H., Maruyama T., Mashiko K. 1974 — Social relation in a small experimental population of *Odontobutis obscurus* (Temminck et Schlegel) as related to individual growth and food intake — Oecologia (Berl.), 17: 187–202.