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# DIFFERENTIATION AND FREQUENCY DISTRIBUTIONS OF BODY WEIGHTS IN PLANTS AND ANIMALS

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The basic and simplest system that one can consider in ecology is a group of individuals of equal age and representing one species, that is, a cohort. This paper is an attempt to show that analysis of such a system may be of great importance to understanding basic ecological problems, such as, intraspecific competition and the dynamics of a single population.

It is easy to observe that in even-aged populations individuals differ in weights. A close look can show that weight distributions in even-aged populations may have different skewness. Most common are distributions with coefficients of skewness greater than zero. Sometimes weight distributions are symmetrical or with skewness coefficients less than zero. In a cohort of growing individuals the coefficient of skewness changes with time: most often starting from zero (symmetrical distribution), it increases in time; sometimes after an initial increase it can decrease in the final stage of growth, which is related to an increased mortality of individuals. The rate of change in skewness, and the skewness itself depend on the density of individuals in a cohort and on food conditions. They are greater at higher densities and increase with deteriorating food conditions. Weight distributions are symmetrical at low densities and optimal food conditions. The differences in individual weights measured by variance of weight distributions or coefficient of variation follow the same pattern, but observed changes with time, density and food conditions are not so clear. These conclusions rest upon the review of numerous papers concerning both plants and animals, which is presented in this paper.

In the past, the properties of weight disributions in even-aged populations were explained not by interactions between individuals, but rather as a natural outcome of the growth process of non-interacting individuals. The exponential equation of growth, with relative growth rate having a normal distribution in populations, was used to support this hypothesis. Obtained weight distributions were of positive skewness; however, this model, which in fact is able to describe the growth process only in its initial stage, cannot explain the changes of skewness of weight distributions with density and food conditions.

A model has been developed which includes competitive interactions among members of even-aged populations to explain observed properties of weight distributions in them. The basic assumption is that intraspecific competition leads to uneven partitioning of resources, which are the object of competition. Functions describing resource partitioning among individuals are included into the model. Two versions of the model are considered: deterministic and stochastic. The first one assumes that the fate of an individual is determined in the early stages of growth and its relative position in the population does not change in time. This corresponds with the situation, for instance, of terrestrial plants or sedentary animals living in a heterogeneous environment. In particular, the mathematical form of the growth model, the so-called balance equation of growth, modified by including a resource-partitioning function, was used. The deterministic model is considered with constant and variable food conditions. In the latter case two situations were analysed: constant in-flow of food and its exponential growth. In the stochastic model of growth it is assumed that for each individual there exists a probability of increasing weight, which depends on past increases in weight. This probability plays the role of the resource-partitioning function. The stochastic model can describe an animal actively hunting for its prey. In both versions, the deterministic and the stochastic one, the dependence of resource intake on the amount of available resource is included.

The skewness of weight distributions given by these models is analysed. It is shown that these models describe and explain all properties of weight distributions in even-aged populations: their skewness and changes in skewness with time, density and food conditions. A set of assumptions on resource-partitioning functions is formulated to obtain observed properties of weight distributions. These assumptions are analysed in detail. An attempt was made to answer the question of whether or not competition is really responsible for differentiation of weights and skewness of their distributions. Restrictions of the models and kinds of organisms described by them are also discussed and ways of verification of the models are presented. Finally, the application of these models of differentiation of individual weights to the construction of non-volterrian models of number dynamics of a single population is suggested.

## 1. INTRODUCTION

A proper description of the number dynamics of a single population means, in fact, a description of the phenomenon of intraspecific competition with all its consequences. From the point of view of the classical approach, the only answer to the question, what is intraspecific competition is the logistic equation of population growth. It can be said that the presence of the term proportional to the second power of number of individuals in this equation is explained by the effect of intraspecific competition on population dynamics. However, the logistic equation says nothing about intraspecific competition. We need a new and different description of this ecological interaction.

One way of doing this is clear. Intraspecific competition always takes place for something: for food, places in space, sexual partners or for some other kind of resources. For individual survival and reproduction it is important to estimate the amount of this resource 'consumed' by each individual. We can start to understand the process of competition if we find its consequences by using a function describing the partitioning of resources among members of the population. The question is then how to construct this function and whether it is possible to find some of its general properties.

One way of solving these problems is to analyse differences among individuals, which often are a result of non-uniform partitioning of resources between them owing to intraspecific competition. First, we should find the variable that would characterize the differences among individuals; then describe some general properties, if they exist, of this variable or its distribution in population; and finally, on this basis, prove some set of assumptions concerning the function of resource-partitioning among population members.

Individual plants and animals of any species differ not only be age and sex: a statement so obvious that it is sometimes forgotten. Instead, we readily notice and generalize interspecific physiological and morphological differences (as in the theory of evolution). This is one of the bases for our conviction that the organic world is complex. Scarce papers on morphophysiological differentiation within populations or species have most frequently been limited to records of variability (see, for example, Yablokov 1966). Only the theory of natural selection and its mathematical formulation, population genetics, admitted intraspecific differences and, in particular, differential survival and reproduction of various genotypes (Fisher 1958) as a fundamental fact. Recently, the problem of intraspecific differences, though from a different point of view from the used in population genetics, appeared in the theory of number regulation in population (Lomnicki 1978, 1980*a*, *b*).

The body weight, one of the most readily measured characteristics, occupies a special position in biological considerations. The whole of bioenergetics is based on weight-related regularities. Power functions of the body weight are used to describe the rate of food consumption in animals (see, for example, Sushchenya & Khmeleva 1967; Sushchenya 1975; Avery 1978), the rate of respiration (see, for example, Duncan & Klekowski 1975) or the rate of reproduction (see, for example, Wootton 1977; Kaplan & Salthe 1979). The rate of changes in individual weight is most often related to the body weight itself (for a review of growth equations see Majkowski & Uchmański (1980)). The above relationships are the result of the conviction that the course of many biological processes depends on the size of organisms, and thus on the body weight. This is a reasonable view as long as it is remembered that the body weight is not the only determinant of these processes (Uchmański 1980*a*).

If we define $A$ as the amount of energy or matter assimilated by an organism per unit time, and $R$ as the total cost of living, then it follows from the energy and mass conservation law that the difference between these two values is equal to the energy or matter that can be used for the production of the body of this organism; this being manifested as a change in body weight, $\Delta w$, or for the production of offspring, $E$, per unit of time, or both:

$$\Delta w + E = A - R. \tag{1.1}$$

The actual weight of an individual will be equal to the sum of weight increases:

$$w = w_0 + \sum \Delta w, \tag{1.2}$$

where $w_0$ is the initial body weight, that is, the weight at birth, sprouting, or at the beginning of any developmental stage. There is an infinite number of combinations in which $\Delta w$ and $E$ can equal the difference between $A$ and $R$. Natural selection means that one of them, maximizing individual fitness, will be established over the lifespan (Stearns 1976, 1980). There are some theoretical premises (Insarov 1975; Ziółko & Kozłowski 1983), supported by many observations, that growth and reproduction do not occur simultaneously on the scale of small time units. Thus, the individual weight of an organism during the period of its growth will be the measure of its energy gains.

The two reasons noted above explain the great importance attached to body weight. There is an unjustified tendency not to perceive that individual organisms, even within a population or an age-class, differ in their weights. There are no premises that would allow us to state that all members of the population, or even of the same age-class, developed or can develop the same strategy for the allocation of energy between growth and reproduction, in terms of both amounts of energy and its distribution in time. Ecological studies also show that the partitioning of resources among members of the population is not uniform. It follows from these arguments that each organism uses differing amounts of energy in different ways. Therefore, differences should be expected in the body weights among individual organisms.

The body weight is one of the components of the phenotype. The differentiation in weight may be expected to be of vital ecological importance if the theory of natural selection is looked upon in the way proposed by Łomnicki (1980*b*). That is, if we agree that genetic and phenotypic characters do not determine the chance of survival and reproduction directly, but only through the rank of an individual in the population, and this rank decides who will survive and who will die under given conditions.

The most natural way of analysing body weights and their differentiation would be to follow the individual fates of an organism, measure its weight at selected time intervals, and compare the results for all individuals. It is easier, however, to ignore some information, and analyse frequency distributions of body weights. The frequency distribution of body weights is a graph, often described by a function, that represents an absolute number of individuals, or a fraction of the total number of individuals, with body weights falling within specified class intervals.

One of the characteristics of this distribution is the average square of the difference in the body weights of paired individuals in a population. It is easy to show that the variance of weight distribution is the measure of the mean square of the differences in body weights between the members of the population. However, the mean square of the difference in body weights does not provide complete information on the structure of body weights in the population, as it may depend on the body weights of the organisms compared. The average square, if the difference is calculated only for heavy organisms, can differ from that for small organisms. The analysis of such regularities provides information on the shape of the frequency distribution of body weights and on its skewness or symmetry. Thus, both these aspects should be considered when the structure of body weights is analysed in a population. The differentiation of body weights, for example, the variance of the frequency distribution of weights, should be analysed along with the shape of this distribution, for example the coefficient of skewness (for detailed definitions of the distribution parameters see Appendix I).

The objective of this paper is to analyse the differentiation and the shape of frequency distributions of body weights in plant and animal populations made up of even-aged individuals, mainly considering the respective patterns and underlying forces. In addition, consequences of differences in body weights of individual organisms in even-aged populations are analysed. Mathematical modelling methods are used throughout the paper. Biological assumptions formulated in the language of mathematics are used for developing a mathematical model. The implications of this model are tested against experimental data.

A biologist–naturalist may feel displeased with the fact that plants and animals are discussed here only indirectly, by analysing the properties of mathematical models. Being used to direct contacts with the object of his study, he will be inclined to protest against mathematical models. He may say that there are too many abstract divagations in them, while too little reality. I would say, however, that these two approaches have much in common. Both naturalists and mathematically oriented biologists develop models. The difference is that these are verbal models of the observed events when constructed by naturalists, and of their mathematical equivalents, when a mathematical approach is applied. The usefulness of these two ways may be discussed, but neither should be discarded (Uchmański 1980*b*).

## 2. Differentiation and frequency distributions of body weights in plants: experimental data

The fact that the relation between the age and size of plants is not unequivocal (White 1980) provides the first indication of size differentiation within plant populations. Hatcher (1963) has found that the two-dimensional frequency distribution of the diameter and age of *Picea mariana* taken from a natural site follows a large asymmetric, bell-shaped curve. Also, in a 300-year-old natural stand of *Acer saccharum* the diameters of stems ranged from 30 to 80 cm (Tubbs 1977). According to White (1980), an unequivocal relationship between the age and size of plants can be expected only in man-managed cultures.

Comprehensive studies on the differentiation and frequency distributions of weights in even-aged plant populations were carried out in Japan in the 1950s. Different plant species were cultivated at variable densities in highly uniform habitats, in which plants were evenly spaced. Standard statistics were used to process the data and unified methods were used to construct frequency distributions of weights (Koyama & Kira 1956).

Kira *et al.* (1956) cultured *Impatiens balsamina* (figure 1). Plants were evenly spaced every 4 cm. On day 16, the frequency distribution of individual weights of complete, live plants was roughly normal, but by day 32 it started to be skewed, the most frequent weight-class being shifted towards a small values. On day 40, the lightest plants were most frequent. The frequency distribution of weights became L-shaped. A similar pattern of changes in the frequency distribution was observed for cultured radish (Koyama & Kira 1956). It was also found that the skewness depended on the density of radishes (figure 2). When radishes were grown 4–8 cm apart, the frequency distributions of their weights on days 21 and 47 were roughly symmetric. In more dense cultures, with plants 2.0–2.8 cm apart, frequency distributions on day 21 were also symmetric, but on day 47 they became skewed, the most frequent being the lightest plants. It was also noted that the mortality of plants is closely correlated with the skewness of weight distribution. It increased from 0 to 48% when the distance between individual plants was reduced from 8 to 2 cm.

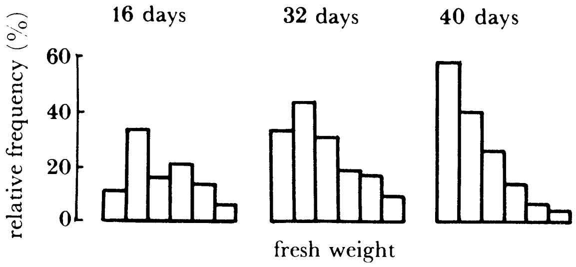

Figure 1. Frequency distribution of total fresh weights in touch-me-not *Impatiens balsamina* at three successive harvests. Plants were spaced by 4 cm. (After Kira *et al.* (1956), redrawn from Koyama & Kira (1956).)

Rose mallow (*Hibiscus moscheutos*) were planted linearly with three different distances between plants (2, 4, and 8 cm) (Kira *et al.* 1956). Shoot length, $l$, and stem diameter, $d$, were measured every five or six days from day 40 to day 70 after sowing. On day 78 all the plants were harvested and their live weights were measured. As the term $d^2l$ was closely correlated with body weight at time of harvest, it was used as an index of plant size. The frequency distribution of plant

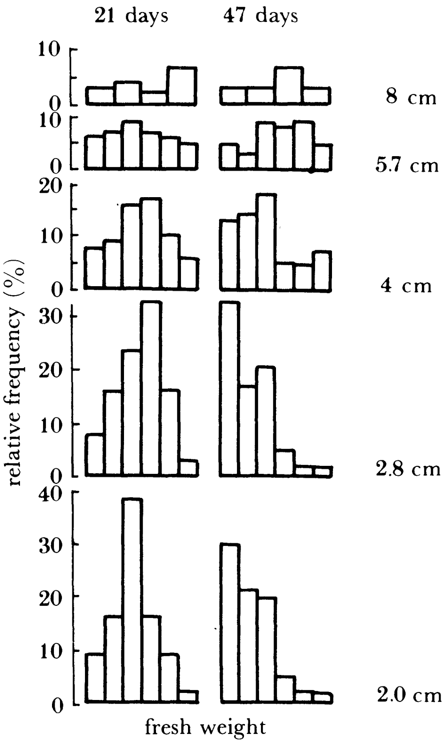

Figure 2. Frequency distributions of fresh weights in radish at 21 and 42 days after sowing in experiments with different distances between plants. (Redrawn from Koyama & Kira (1956).)

seed weights was normal. However, the frequency distributions of plant weights were positively skewed, the most frequent class being shifted to the left with age (figure 3). This process was more rapid and started earlier at higher densities. The same results were obtained in experiments with soybean (Koyama & Kira 1956), though the rate of change in the frequency distribution of weights was different owing to species-specific differences and as a result of differences in spacing. A close correlation was also found between the density of plants (that is, skewness) and their mortality.

The distributions of tree diameters at breast height for 13-year-old pines *Pinus densiflora* at four densities have been presented by Satoo *et al.* (1955). Koyama & Kira (1956) recalculated these data per trunk volume, which was proportional to the basal area, by using the formula: basal area = (diameter at breast height)$^2$ $\pi/4$. At the lowest densities, the frequency distributions of weights estimated in this way were approximately normal or slightly skewed, while at the highest densities they were L-shaped (figure 4). Again a close correlation was found between mortality and the density of tree stands. In all cases the distributions of diameters at breast height were approximately normal. Kira *et al.* (1956) obtained identical results for a nine-year-old pine forest. Kira *et al.* (1956) also cultivated ragweeds *Ambrosia elatior* in two different ways: 29 individuals per square metre of fertile soil and 243 individuals per square metre of very poor soil. The two frequency distributions of weights were L-shaped, but the dominance of the lowest class was more pronounced on poor soil (figure 5). The two frequency distributions of the heights of plants were symmetric, as in the study of a nine-year-old pine stand quoted above. Similar results were obtained for such plants as *Erigeron linifolius* and *Cerastium caespitosum*.

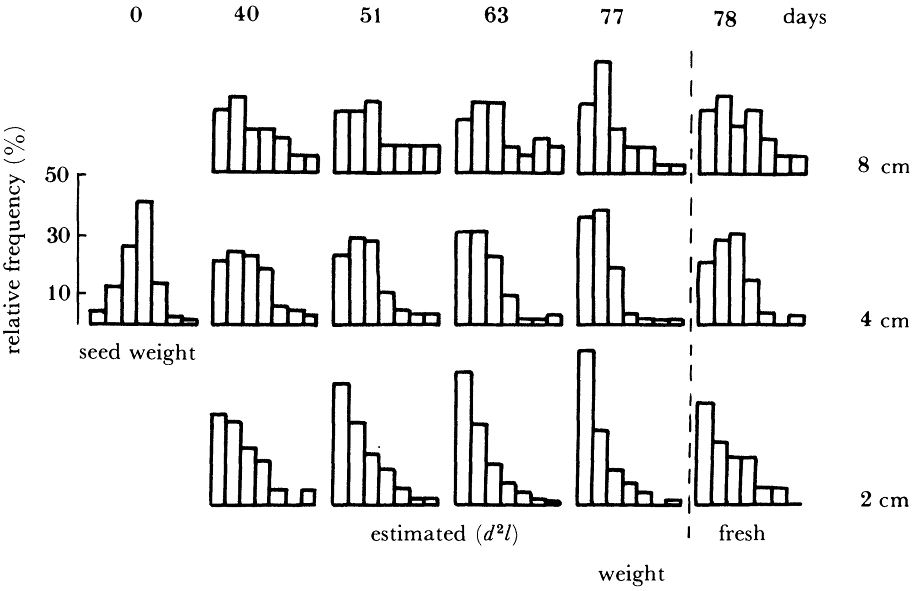

FIGURE 3. Frequency distributions of seed weights, estimated plant weights ($d^2l$) and fresh weights of plants (78 days after sowing) in rose mallow *Hibiscus moscheutos* at five successive harvests. The experiment was conducted with three different spacings between plants. (After Kira *et al.* (1956), redrawn from Koyama & Kira (1956).)

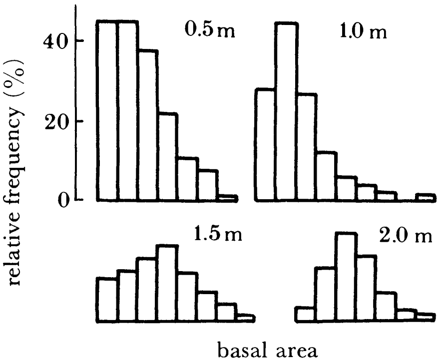

FIGURE 4. Frequency distributions of basal areas ($\frac{1}{4}\pi \times$ (diameter at breast height)$^2$) of 13-year-old Japanese red pine *Pinus densiflora* artificially planted at four densities: distances between plants are indicated. (After Satoo *et al.* (1955), redrawn from Koyama & Kira (1956).)

Slightly different results were obtained in other experiments with the soybean (Kira *et al.* 1953). Seeds and early developmental stages of this plant had normal distributions of weights. In later stages the distributions were L-shaped, but their skewness did not seem to depend on density (figure 6). The least dense cultures, with plants 20–30 cm apart, had skewed distributions at the end of the experiment on day 119, while in the more dense culture, with plants 15 cm apart, the weight distribution was still symmetric on that day. The densest culture, with plants 5 cm apart, had a rectangular distribution on day 45. This variant could not be continued because of heavy rains.

Similarly, the weight distribution of the turnip was normal over the two months of the experiment (figure 7) (Kira *et al.* 1953). Slightly skewed distributions were obtained at the

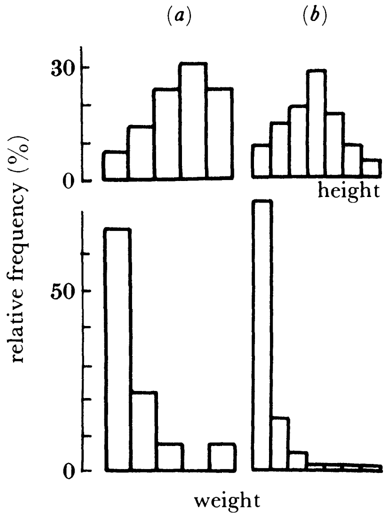

FIGURE 5. Frequency distributions of plant heights and weights of ragweed *Ambrosia elatior* grown in two different conditions: (*a*) on fertile soil; (*b*) on poor soil. (After Kira *et al.* (1956), redrawn from Koyama & Kira (1956).)

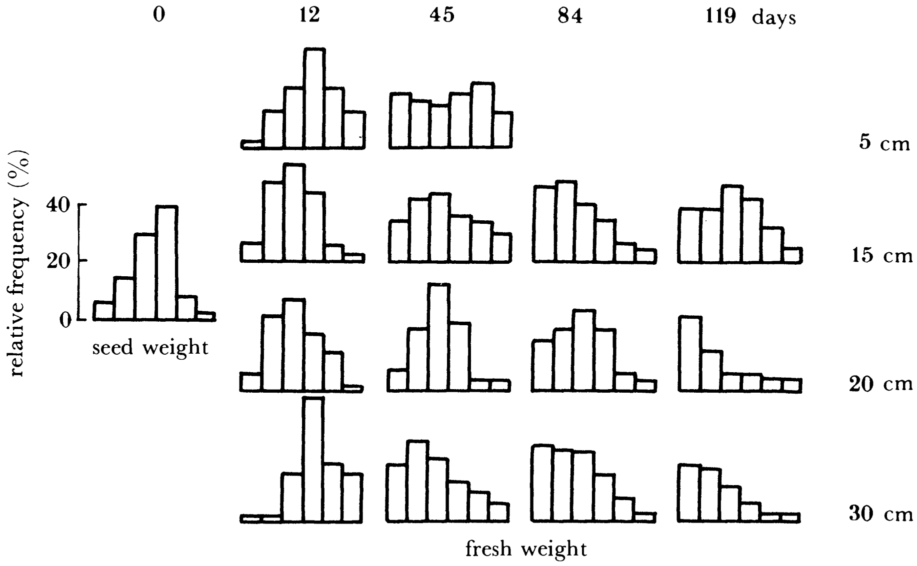

FIGURE 6. Frequency distributions of seed weights and fresh plant weights in soybean at successive harvests. Plants were sown at four different densities: distances between plants are indicated. (After Kira *et al.* (1953), redrawn from Koyama & Kira (1956).)

highest densities. All plants survived. No correlation was found between the density and skewness of weight distribution, except for the highest density, in other experiments, with the bean *Phaseolus chrysanthos* var. Dainagon (Kira *et al.* 1956), but the mortality of plants was also low. Hozumi *et al.* (1955) estimated the weight of the dent corn by multiplying the length of the stem by the square of its circumference and found that the weight distribution was almost symmetric at the end of the experiment (figure 8). The variability of these estimated weights (calculated from the formula: (maximum weight − minimum weight)/mean weight) increased with time especially for high-density cultures.

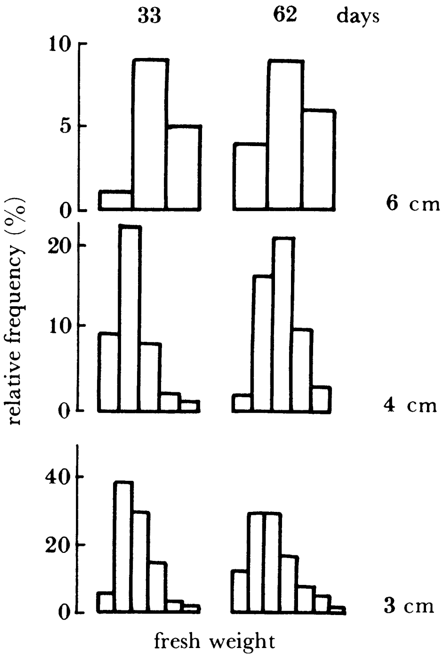

Figure 7. Frequency distributions of fresh plant weights of turnip at two successive harvests. Plants were sown at three different spacings. (After Kira *et al.* (1953), redrawn from Koyama & Kira (1956).)

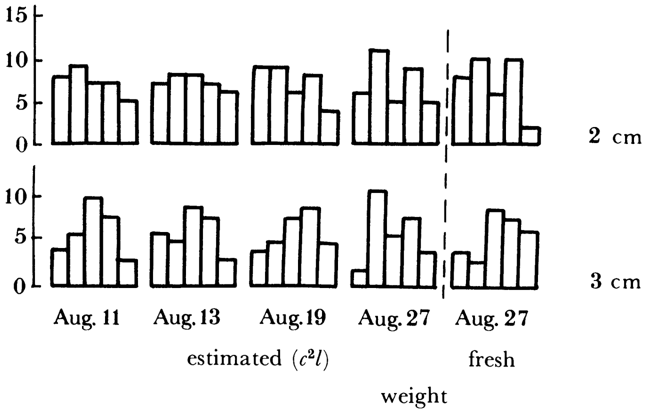

Figure 8. Frequency distributions of estimated plant weights and those actually measured (at the end of the experiment) in dent corn in successive harvests at two densities. (After Hozumi *et al.* (1955), redrawn from Koyama & Kira (1956).)

These Japanese works were forgotten for over ten years. In the 1960s similar experiments were done. Obeid *et al.* (1967) grew the fibre flax *Linum usitatissimum* at three densities (60, 1440 and 3600 seeds per square metre). Seeds were broadcast evenly over homogeneous plots. Three harvests were taken: two weeks after seedling emergence; six weeks after emergence and at maturity. The dry weight of above-ground parts of the plant was measured. The frequency distribution of individual plant dry weights was symmetric for the first harvest at low and medium densities (figure 9); at high density it was sightly positively skewed. At the second harvest the frequency distribution at low density remained symmetric, but at medium and high densities the frequency distributions were skewed (particularly at high density). At the third

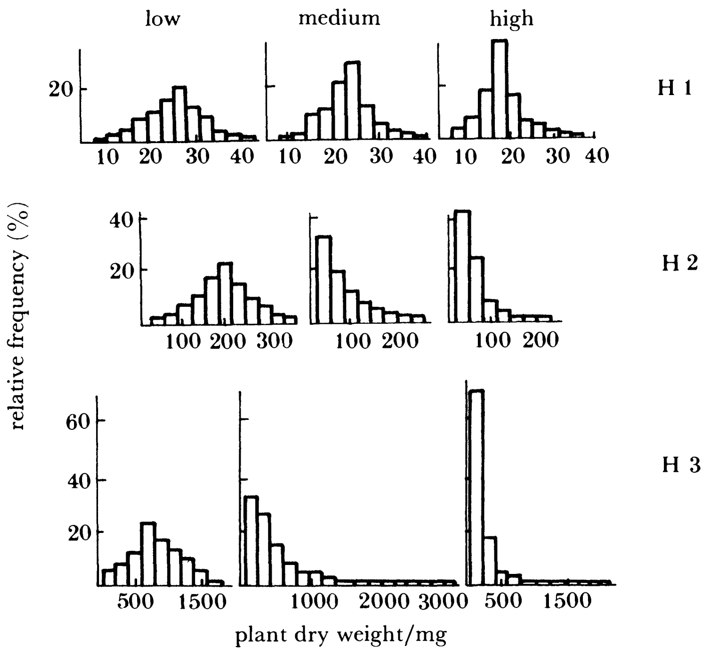

FIGURE 9. Frequency distributions of individual plant dry weights in fibre flax *Linum usitatissimum* at three successive harvests (H1, H2, H3) in three densities (low, medium, high). (Redrawn from Obeid *et al.* (1967).)

harvest the frequency distribution at low density was practically symmetric; at medium and high densities the skewness markedly increased compared with that at the second harvest, being the highest at high density. In this variant the frequency distribution approached a log-normal curve. It should be noted that in all variants mean weight of individual plants decreasing with growing density. However, the frequency distributions of individual seed weights were symmetric with equal means for the three densities, with variance only higher at high density.

Ogden (1970) investigated mixed annual herb communities colonizing an arable field. Weight frequency distributions for particular species (*Atriplex patula*, *Polygonum aviculare*, *Poa annua* and other Graminae, *Stachys arvensis*, *Stellaria media*, *Spergula arvensis*, *Senecio vulgaris*, *Polygonum persicaria*, *Polygonum lapathifolium*) and also for other species together (*Matricaria matricarioides*, *Capsella bursapastoris*, *Fumaria muralis* ssp. *boraei*, *Anagalis arvensis*, *Veronica officinalis*, *Geranium molle*, *Sonchus oleraceus*, *Ranunculus repens* and *Taraxacum officinale*) were markedly skewed in favour of small individuals (figure 10). Some of these frequency distributions were log-normal. It should be noted that the frequency distributions of individual heights were normal in all cases.

White & Harper (1970) did experiments with the turnip *Brassica napus* and the radish *Raphanus sativus* (figure 11). These two species were grown in pure cultures and in mixed cultures with equal proportions of both species. Two densities were used: 28 and 72 plants per unit area. The experiment was continued for 12 weeks. In this time the frequency distribution of individual weights was examined three times. At low densities, the skewness of the frequency distribution of weights declined with time for the turnip, and was stable for the radish; while in mixed cultures a slight increase in skewness was observed. At high densities a sharp increase in skewness occurred between the first and second harvests then skewness slightly increased or was stable. In all cases, however, the frequency distributions were more skewed at high than

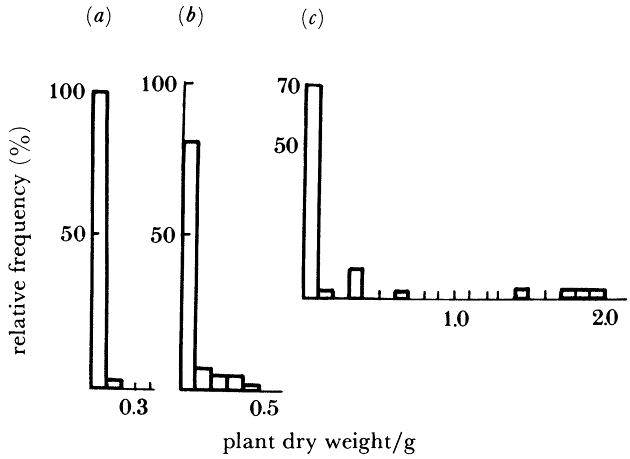

FIGURE 10. Frequency distributions of individual plant dry weights in mixed weed populations: (*a*) for *Graminae* mostly *Poa annua*; (*b*) for *Atriplex patula*; (*c*) for *Polygonum aviculare*. (Redrawn from Ogden (1970).)

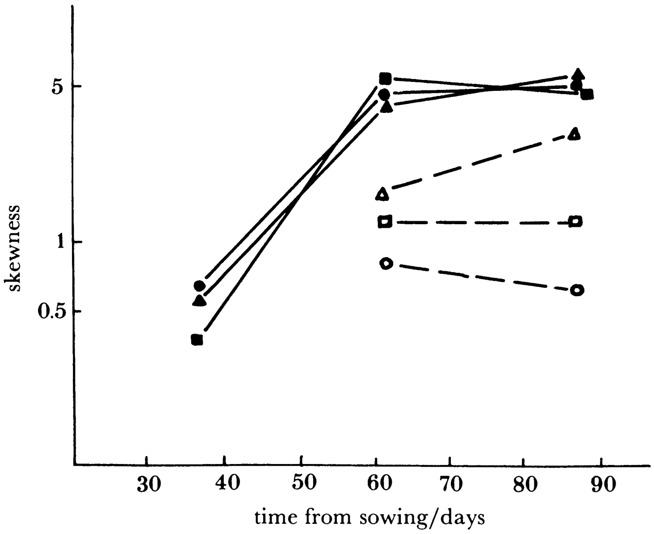

FIGURE 11. Changes of skewness of weight distribution with time in *Brassica napus* (circle), *Raphanus sativus* (square) and mixture of both (triangle) in experiments with low (open symbols) and high (closed symbols) densities. (Redrawn from White & Harper (1970).)

at low densities. At high density the number of plants gradually dropped as the lightest plants died. This may explain why skewness did not increase at high density after the second harvest.

Most of the patterns of the frequency distribution of individual plant weights in experimental cultures were also observed in natural populations. Heyward (1939) analysed frequency distributions of tree diameters at breast height in forest communities of Florida, Georgia and Alabama subject to seasonal fires. Trees of these stands, several tens of years old, were burned a dozen or so years before the study. Two groups of trees could easily be distinguished, and corresponded to some degree with age classes: those 1–6 inches (2.5–15 cm) in diameter had mostly been destroyed by fire, but bigger trees, 6–20 inches (15–50 cm) in diameter, had suffered less from fire. In the first group, including such species as wax myrtle *Myrica cerifera*, water oak *Quercus nigra* and flowering dogwood *Cornus florida* most of the diameter frequency distributions were L-shaped, highly skewed. But this group also includes the laurel oak *Quercus laurifolia*, the distribution of which was skewed in the opposite direction, with the biggest trees being most abundant. The group of bigger trees (loblolly pine *Pinus taeda*, longleaf pine *Pinus pallustris* and slash pine *Pinus caribaea* on one stand) was partly composed of trees exhibiting negatively skewed frequency distributions of diameters. However, on one site the frequency distribution of diameters for the slash pine and on another site for longleaf pine, were positively skewed, that is, lighter trees predominated. The species composition of stands on the other sites was similar, but as they were burned in much more distant past, it was not possible to distinguish clear-cut groups of bigger and smaller trees. The frequency distributions of diameters for most of the species in these communities were positively skewed to different degrees, ranging from L-shaped distributions to unimodal slightly skewed distributions for various species. Only on a few stands was the diameter frequency distribution for the longleaf pine slightly negatively skewed, though this was in communities less uniform with respect to age.

Daubenmire (1968) performed similar studies in Minnesota and Idaho on populations including some percentage of individuals of different ages. In Minnesota, for all but one species (*Ulmus americana*), the frequency distributions of diameters at breast height were L-shaped; this was the case for species permanently occupying these sites (*Acer saccharum*, *Tilia americana*, *Ostrya virginiana*, *Quercus rubra*, *Fraxinus americana* and *Quercus macrocorpa*) and for the remains of earlier successional stages (*Populus tremuloides*, *Betula papyrifera*, *Pinus strobus*). For the communities growing in Idaho the frequency distributions of diameters were also positively skewed. This was shown for *Abies grandis* and *Pseudotsuga manziesii*. The same author (Daubenmire 1968) also gives diameter distributions for *Abies losicarpa* in Wyoming, *Stipa comata* in Washington, *Abies grandis* in Oregon and *Terragastris altissima* from Surinam (data for this last species after Schultz (1960)). All the frequency distributions were L-shaped.

Hett & Loucks (1971) analysed frequency distributions of diameters at breast height for the sugar maple *Acer saccharum* on nine sites in Wisconsin that differed in age, history, natural conditions and location. All the frequency distributions were L-shaped. The class of smallest trees was most abundant, and the successive classes of increasing sizes were represented by declining number of trees. On three sites located in the southern part of this state skewness increased with age. The same authors (Hett & Loucks 1976) obtained similar diameter distributions for balsam fir *Abies balsamea* and hemlock *Tsuga canadensis* on different sites.

Ford & Nowbould (1970, 1971) have found skewness coefficients greater than zero for frequency distributions of squared stem diameters of the sweet chestnut *Castanea sativa* in natural stands. This was the case for all groups of even age, ranging from one-year-old to 18-year-old trees. Most of the distributions were L-shaped. Later studies carried out by Ford (1975) provided much new information on the size structure in even-aged monocultures. Skewed frequency distributions of diameters, with the skewness coefficient greater than zero, were observed in all *Picea sitchensis* populations, this coefficient being higher for initially dense stands (figure 12). Changes in skewness with age were irregular. No regular trends could be seen for populations 29, 34 and 36 years old. Ford also conducted similar experiments for annual plants such as *Tagetes erectus*, *Sinapsis alba* and *Lycopersicon esculentum*. All the frequency distributions of individual weights were skewed, the coefficient of skewness being greater than zero. In additional studies on *Tagetes patulus* skewness was greater in cultures with higher initial densities; it also increased between weeks 2 and 6, while it declined in week 8 of the experiment (figure 13).

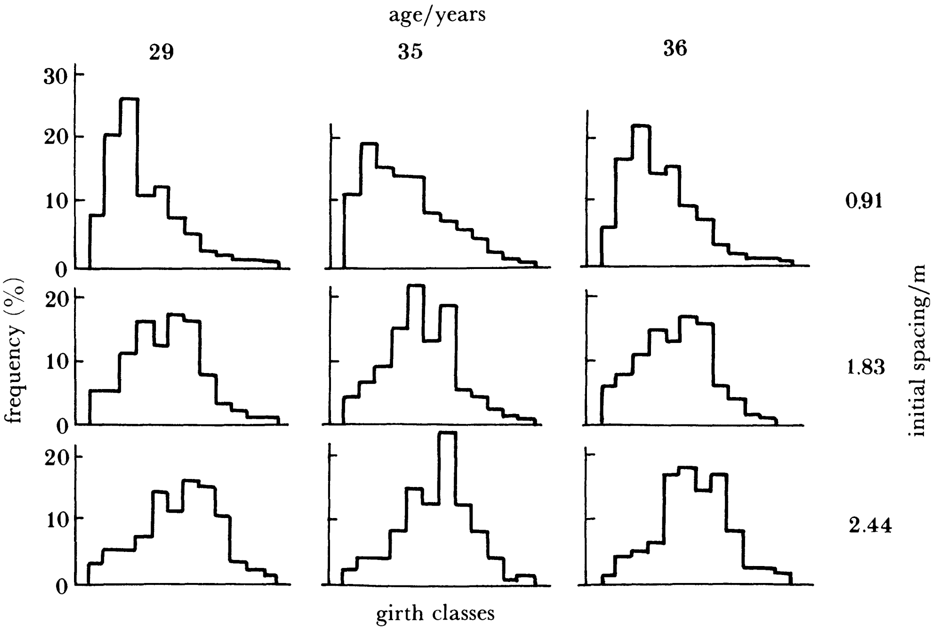

Figure 12. Changes with age of distributions of girth in three populations of *Picea sitchensis* established at different initial planting intervals. (Redrawn from Ford (1975).)

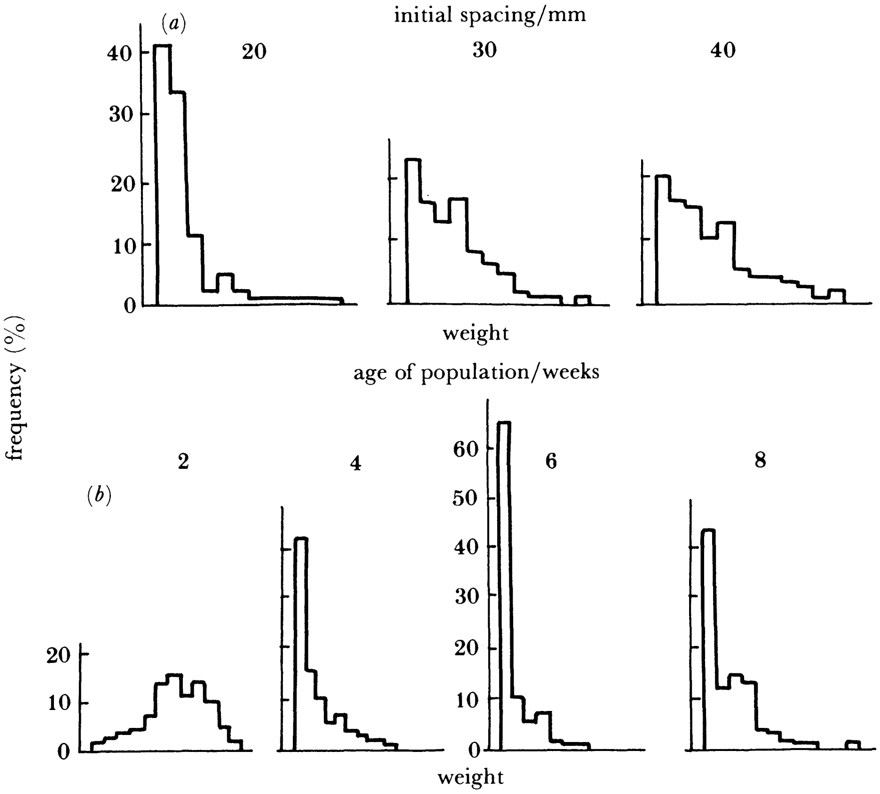

Figure 13. Frequency distributions of weights in *Tagetes patula*: (*a*) relation between initial spacing of plants and the shape of weight distribution at day 56 of the experiment; (*b*) changes of the weight distribution with age. (Redrawn from Ford (1975).)

Ford (1975) emphasized one more feature of the frequency distribution of plant weights. In his opinion, the appearance of two peaks in the frequency distribution of individual weights is a more important index of competition than skewness. One well-pronounced peak developed in the class of lightest plants and the other one, not so conspicuous, was in the range of medium weights.

It follows from a similar study carried out by Jack (1971) on firs growing in different densities that the frequency distributions of tree volumes, as calculated from the measurements of height and diameter, become skewed with increasing density, and the average volume of trees decreases. The number of trees in volume classes had beta distribution.

Mohler *et al.* (1978) have found that for natural stands of the pine cherry *Prunus pensylvanica* and balsam fir *Abies balsamea* the frequency distribution of individual tree weights is positively skewed, most frequently L-shaped, for young, three- to four-year-old trees, and then the skewness drops with time. The distribution of weights in trees a dozen or so years old (balsam fir) or several tens of years old (pine cherry) becomes almost symmetric (figure 14). According to these authors, the reason for this lies in the fact that at this age the population undergoes a natural drastic thinning, and as a result trees grow in declining densities from year to year. They presented a general pattern for changes in the shape of weight frequency distributions in even-aged natural trees populations (figure 15). Frequency distributions of the weights of seeds and very young plants most often are symmetric. With time they develop a positive skewness as a result of competition, but also without competition, as an intrinsic property of growth itself. When the highest skewness is reached, the process of natural thinning begins, with mostly the lightest individuals being eliminated. As a result the density of plants declines and competition is reduced. In consequence, skewness disappears, and after some time the frequency distribution may become symmetric. This pattern differs from the monotonic increase in weight distribution skewness with time, proposed in the Japanese works discussed earlier. It is consistent with the results obtained by Kohyama & Fujita (1981) for almost even-aged natural populations of *Abies* (*Abies veitchii* and *Abies mariesii*), in which the frequency distribution of tree diameters at one-tenth of the tree height became less skewed with time owing to natural thinning of the population.

Positively skewed frequency distributions of individual weights are also observed in aquatic plants. Seed & O'Connor (1981), who studied the fauna associated with marine macroalgae of the tidal zone in coastal areas of Great Britain, analysed frequency distributions of individual weights for the seaweed *Fucus serratus*. These distributions were markedly skewed, with dominance of light plants, and the heaviest plant class being distant from the most frequent class.

Polish literature dealing with the structure of individual size in even-aged plant populations is rather poor. Jedliński (1929) analysed frequency distributions of tree thickness in three spruce stands differing by age but covering similar sites. All distributions were significantly skewed, with most individuals in medium classes. The skewness of the frequency distribution of tree thickness significantly increased with age in stands 50, 70 and 100 years old. At the same time, the variance of the distribution increased with a changing number of trees in the population with time. Also Paczoski (1930) analysed the frequency distribution of individual tree thickness in a pine–spruce stand. It was symmetric for both these species. These two papers, with a short discussion of the structure of size in tree stands, are quoted by Obmiński (1977). The same author refers to Ilvessalo (1923, quoted in Obmiński (1977)), who analysed the frequency

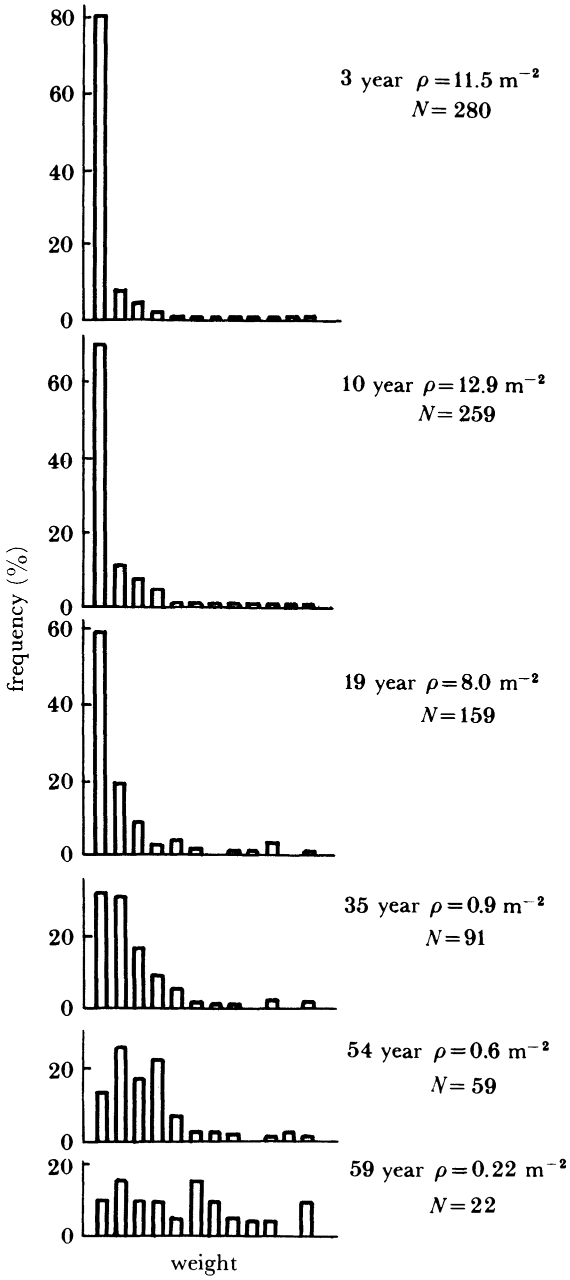

FIGURE 14. Changes of frequency distribution of above-ground plant weights in *Abies balsamea* with age. Symbol $\rho$ indicates stand density; $N$, number of individuals. (Redrawn from Mohler *et al.* (1978).)

distribution of tree thickness in 70-year-old pine stands growing on sites of increasing quality. Unfortunately, we do not know the densities of trees in these stands. On the poorest site the distribution was positively skewed, similar in shape to that obtained by Jedliński (1929). On the two other, relatively better sites, the frequency distribution of individual weights was symmetric. The variance of these distributions was higher for the two better sites.

Recently Kimsa (1980) presented frequency distributions of tree thickness for three 70-year-old pine stands. In two cases they were positively skewed, as above, and in the third

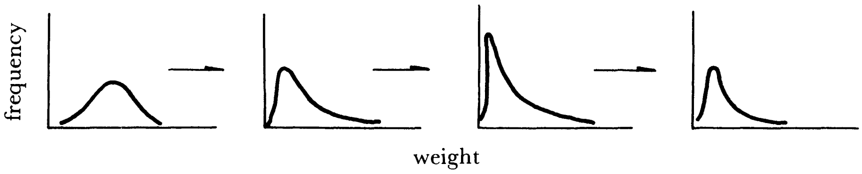

FIGURE 15. Theoretical pattern of changes of weight distribution with age in natural stand proposed by Mohler *et al.* (1978). (Redrawn from Mohler *et al.* (1978).)

case the distribution was bimodal. Though the age of these stands was well defined, it cannot be discounted that some younger trees were present there, as it is indicated by bimodal distribution obtained by Kimsa (1980). Nevertheless, each of the two parts of the bimodal distribution, which probably groups individuals of similar age together, is positively skewed and of the shape described above.

A more detailed analysis of frequency distribution in plant size is give by Czarnowski (1978). He argues that the frequency distributions of individual plant sizes are most often normal, thus symmetric, however he does not consider the effect of population density or site conditions on the distribution shape. He only found some patterns concerning changes in the variance, related to age and density in even-aged plant populations. For a New Zealand population of the pine *Pinus radiata* he obtained

$$\sigma^2 = \varphi(1+N)^2, \tag{2.1}$$

where $\sigma^2$ is the variance of the frequency distribution of diameters at breast height, $N$ is the density and $\varphi$ is a constant. It follows from (2.1) that the diversity of plant sizes, as measured by the distribution variance, increases as the square of density. On the other hand, the author noticed that in even-aged plant populations the variance increased with age as well.

In this section the frequency distributions of individual plant weights have been discussed. In some cases the weight was replaced by the diameter of trunks or stalks, circumference or diameter at breast height, or by the trunk volume, on the assumption that these measures are proportional to plant weight. Some comments should be added on the frequency distribution of individual plant heights. According to Harper (1977), who reviewed the scarce literature available on the frequency distribution of heights in terrestrial plants, these distributions are symmetric, most often normal, sometimes negatively skewed, no matter how skewed the frequency distributions of individual weights are (figure 16). This situation suggests, as Harper (1977) argues, that at least some light plants, which predominate by number in the populations with positively skewed weight distributions, are capable of counteracting the effect of competition by reaching and maintaining heights comparable to those of their heavier competitors. Such a possibility of compensation is closely related to the ‘way of life’ of terrestrial plants. It is not available for animals. They cannot modify their position resulting from the frequency distributions of their weights in such an obvious way, through increasing their linear dimensions. Because of this we restricted our interest to weight distributions only for plants, but in the next section, dealing with frequency distributions of individual sizes in animals, we will discuss the frequency distributions of both linear dimensions and weights.

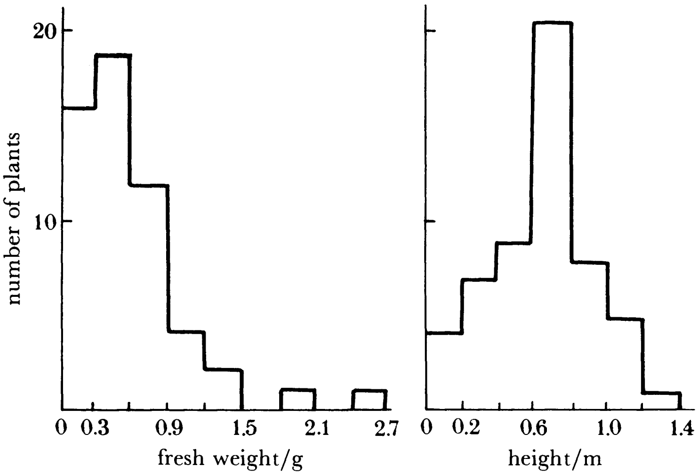

Figure 16. Comparison of frequency distributions of plant weights and heights in a natural stand of *Elatostema rugosum*. (After Ogden (1970), redrawn from Harper (1978).)

## 3. Differentiation and frequency distributions of body weights in animals: experimental data

Studies on the frequency distribution of individual weights in animals are very scarce. Laboratory or field experiments on weight distribution in even-aged animal populations are almost completely lacking. Most records have been taken during work on another subject, and they illustrate frequency distributions of body weights (sometimes body length), mostly in samples of diverse age structure, taken from natural populations.

DeAngelis *et al.* (1980) raised one-year-old largemouth bass *Micropterus salmonides* in two tanks. The frequency distributions of body lengths were similar in the two tanks at the beginning of the experiment, showing a high positive skewness (figure 17). The number of small fish in successive classes of weights rapidly increased, and after reaching a maximum, declined, first violently, then very slowly, producing a long 'tail' for classes of biggest fish. Fish in one tank were supplied with adequate amounts of *Daphnia* spp., while in the other they were not supplied with food at all, and cannibalism occurred, the intensity of which was dependent on the size ratio between the prey and predator, smaller fish being eaten by bigger ones. The character

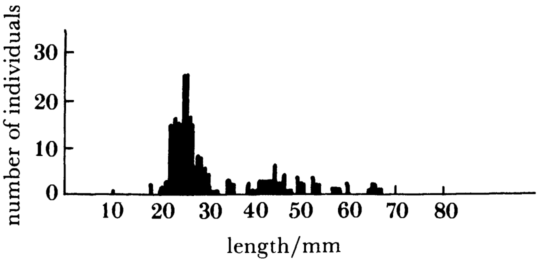

Figure 17. Length distribution of young-of-the-year largemouth bass *Micropterus salmonides* at the beginning of the experiment. (Redrawn from DeAngelis *et al.* (1980).)

of the frequency distribution of body lengths remained unchanged throughout the experiment in the two tanks, although the average fish length almost doubled and the total number of fish largely declined, particularly in the tank of unfed fish. All the time the frequency distributions had skewness coefficients greater than zero.

Beamish & Chilton (1982) presented two-year data concerning changes over time in length distribution for the sablefish *Anoplopoma fimbria*. There are no clear patterns in changes of distributions, however there are some distributions with skewness greater than zero. The authors discussed the paper by Kennedy & Smith (1972) and cited length distribution of a one-year-old generation of this species: it has a skewness greater than zero (figure 18).

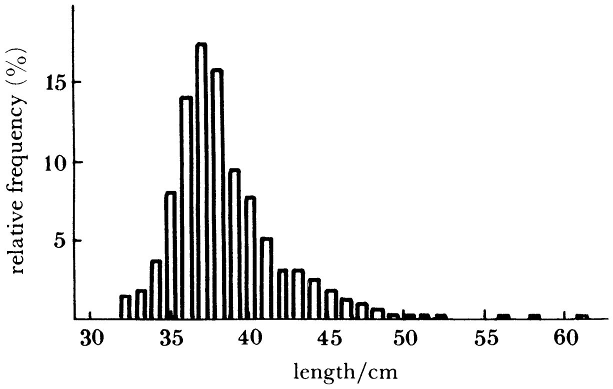

FIGURE 18. Length distribution of the sablefish *Anoplopoma fimbria* at the age of one year. (After Kennedy & Smith (1972), redrawn from Beamish & Chilton (1982).)

Wilkońska (1975) analysed frequency distributions of body length in roach fry of the August generation from Żarnowieckie Lake and from two other lakes. Though rather superficially presented, they are of an approximately symmetric shape. Positively skewed frequency distributions of lengths for older roach as well as lengths and weights for perch from Żarnowieckie Lake were obtained by Ciepielewski (1975) on the basis of fish caught by fishermen. The significance of these studies is partly obliterated by the fact that the samples to some degree consisted of uneven-aged fish.

Interesting results on the effects of liming, used to counteract water acidification in southwestern Sweden, on the salmon *Salmo salan* population are presented by Bengtson *et al.* (1980). During the periods of heavy acidification only one-year-old salmon were present in catches, and their length distribution was positively skewed. After liming, the population returned to the state observed long before intense acidification. The total number of individuals increased, two generations appeared (one and two years old) and skewness of length distribution was reversed for the one-year-old generation and it remained greater than zero in the two-year-old generation. The same paper characterizes the effect of liming on the perch *Perca fluviatilis* population. Before treatment only a few large individuals were caught. Their body lengths were evenly distributed between 30 and 40 cm, After liming large numbers of young fish appeared, with positively skewed length frequency distribution.

In other experiments on growth in fish, the coefficient of variability and variance were measured for frequency distributions of body weights or lengths. Włodek (1971) analysed the biomass and fry production of the Polish race of the carp in ponds at Gołysz. Some of these ponds were not supplied with fertilizers, and some others were enriched with phosphorus or with a mixture of phosphorus and nitrogen. Early in July 1967, 2600 fish of an average individual weight of 2 g were introduced to each of these ponds. Samples of fish were noted every ten days to the end of September, and some biometrical measurements were taken. In all the ponds the coefficient of weight variability was higher than the coefficient of length variability. Mean variability coefficient calculated for all the samples was greater for unfertilized than for fertilized ponds. Considering each sample separately, the variability coefficient of individual weights was higher in unfertilized ponds compared with fertilized ones for about half the total number of samples. It may be suggested, therefore, that the increase in the available food supply in fertilized ponds accounts for the unification of growth compared with the situation in unfertilized ponds with a more limited food supply. The lowest variability was observed at the beginning of the experiment. In successive samples the variability coefficient increased, most rapidly in unfertilized ponds, which implies that the differences in fish weight appeared there the earliest. In all cases, the variability coefficient reached a maximum during the period of negative production in the population, that is, when starving fish were losing weight. The author obtained a statistically significant negative correlation between production and variability coefficient of individual fish weights in unfertilized ponds.

Similar results are also reported by Laurence (1977, after Beyer & Laurence (1980)). Individual fry weight of the winter flounder *Pseudopleuronectes americanus* reared with a constant food supply and at constant temperature increased from 14 μg at the beginning to 151 μg at the end of the experiment. Standard deviation of the weight distribution continuously increased from 3.3 to 80 μg, respectively, which means that the variability coefficient increased from 0.24 to 0.53.

Similar patterns were also observed in crustaceans. Prus (1977) analysed frequency distributions of the body weight of *Asellus aquaticus* in samples taken more than ten times over three seasons. They were positively skewed, though they contained individuals of different ages. But owing to the information on the percentage of particular age-classes in the samples, it can be stated that in the periods when one of the age-groups dominated by number, the frequency distributions were also positively skewed.

Kolding & Fenchel (1979) examined frequency distribution of body length in three groups of age and sex (juvenile forms, males and females) during the life span of one generation for another crustacean, *Gammarus oceanicus*, living in salt waters off the Danish coast. The distributions for juveniles were positively skewed all the time, except in September, which is the last month of occurrence of this developmental form. The first adults appeared in October. During the first two months the frequency distribution of body lengths in males was either negatively skewed or symmetric, and then became positively skewed by February. The frequency distributions of female length were either symmetric or negatively skewed all the time.

The coefficient of skewness is greater than zero in the case of length distribution for another crustacean *Mysis mixta*, which was investigated in the shore waters of New Hampshire by Grabe & Hatch (1982) (figure 19).

Diaz (1980) presented frequency distributions of body weights of the crab *Emertia talpoida*. Though the population consisted of individuals differing by age, the successive generations were represented in these distributions by single peaks, therefore it was possible to assess that frequency distributions of weights in even-aged groups had a skewness coefficient greater than zero.

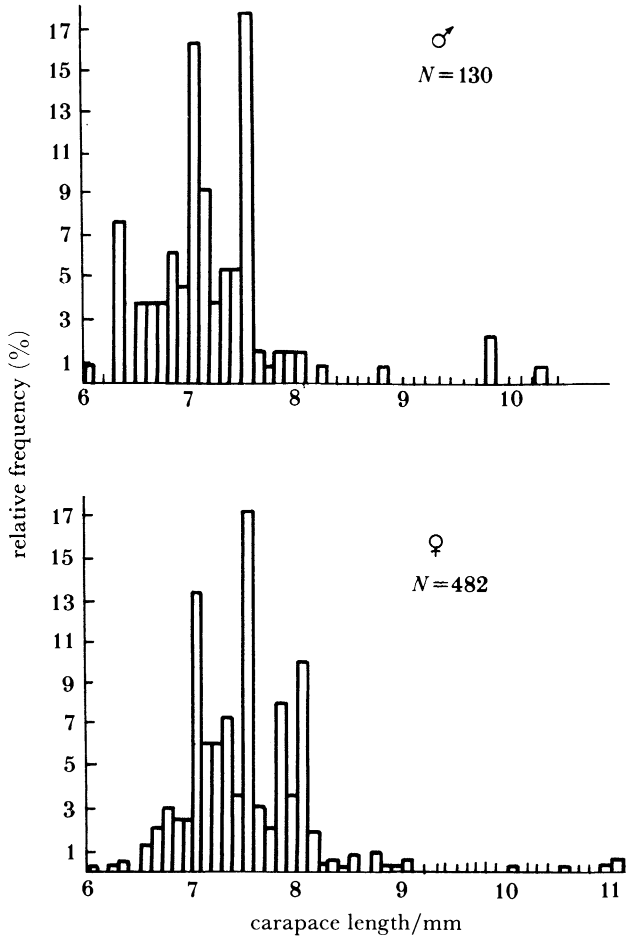

FIGURE 19. Frequency distribution of carapace length for sexually mature (males and females) *Mysis mixta*. (Redrawn from Grabe & Hatch (1982).)

Parry (1982) investigated a few species of molluscs in the coastal waters of Australia. The length distribution for individual *Notoacmea petterdi* under poor food conditions, but not suffering starvation, had positive skewness during almost the whole period of observation. The distributions for *Patella peroni* were symmetric or negatively skewed. But according to the authors this species was not suffering from starvation. The species *Cellana tramoserica* and *Patelloida alticostata* had a period of starvation, and this is the reason for high mortality, which together with the presence of predators, may explain the negative skewness of length distribution for individuals of these species.

Wilbur & Collins (1973) obtained a positively skewed frequency distribution of body weights for the frog *Rana sylvatica* and the salamander *Ambystoma maculatum*. The skewness of the frequency distribution of tadpole weights of *R. sylvatica* at 50 days old was significantly related to the initial density of animals (figure 20). The highest skewness occurred at the highest initial densities, and the coefficient of skewness declined with decreasing initial densities. At high initial densities of tadpoles, the skewness of weight distribution markedly increased with time, while the mean weight increment was very low so that only a few tadpoles underwent metamorphosis (figure 21). Then, at low densities, a rapid growth was observed at the beginning: a high

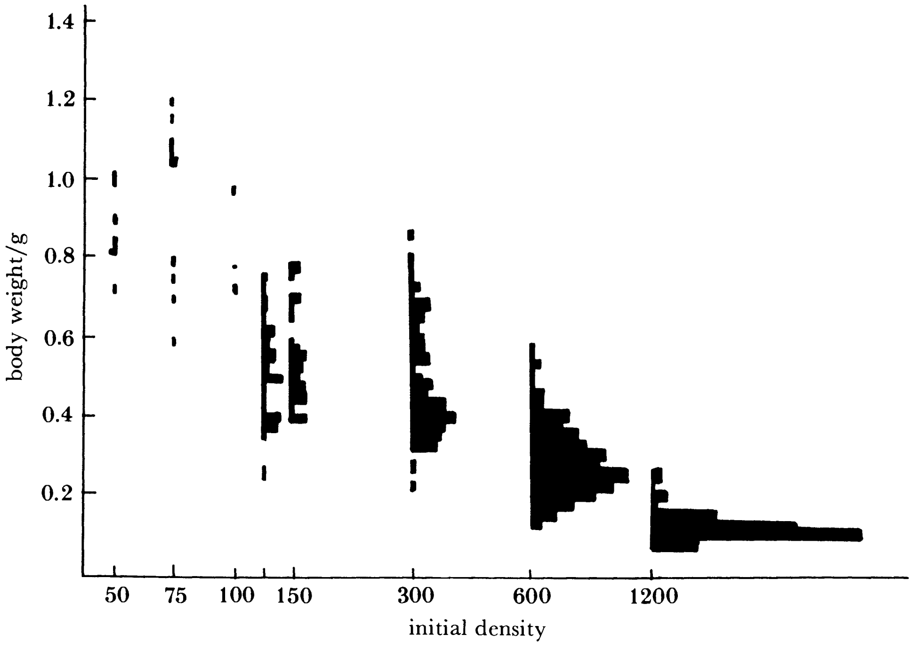

FIGURE 20. Frequency distributions of body weights of *Rana sylvatica* larvae at various initial densities at day 50 after the start of the experiment. (Redrawn from Wilburn & Collins (1973).)

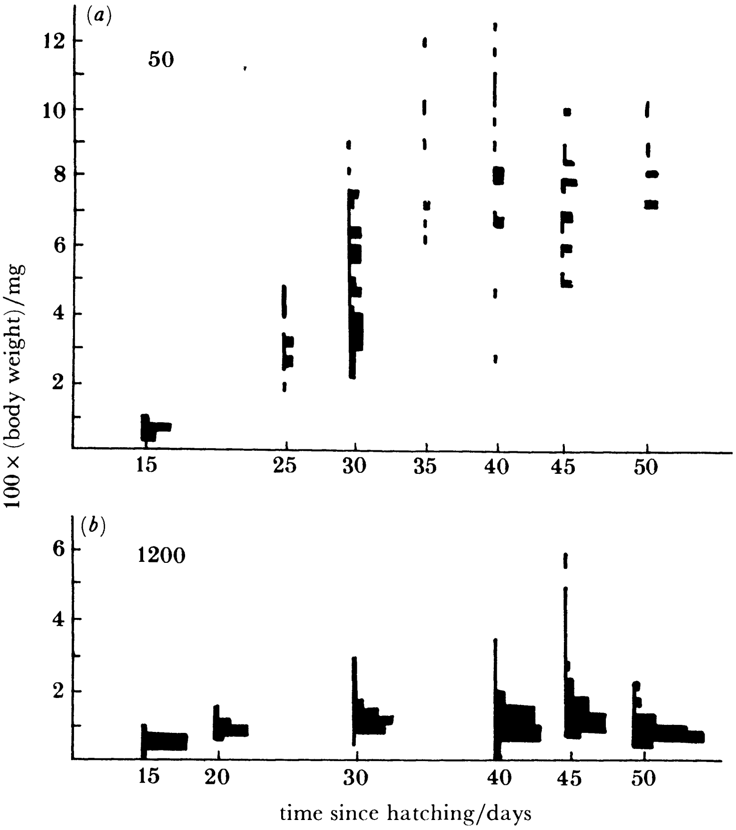

FIGURE 21. Frequency distribution of body weights of *Rana sylvatica* larvae in two populations of initial densities 50 (*a*) and 1200 (*b*) larvae at selected times after the start of the experiment. (Redrawn from Wilburn & Collins (1973).)

variance in body weights, and irregular but approaching uniform weight frequency distributions. These relationships were less clear-cut for the salamander *A. maculatum*. As Collins (1979) has found, the tadpoles of *Rana castesbeiana* also had a skewness coefficient greater than zero at the time of metamorphosis.

Loman (1978) analysed length distributions in different age-classes of the frogs *Rana arvalis* and *Rana temporaria*. There were distinct shapes of the length distribution curve only for frogs that survived no more than one winter. For *R. arvalis* it was almost symmetric, while for *R. temporaria* of the first age-class it was positively skewed for most of the time. Very few individuals of older age-classes were caught, and the frequency distribution of their weights was irregular.

Mazurkiewicz (1972) analysed the frequency distribution of individual weights for male bank voles *Clethrionomys glareolus* of all age-classes, except the oldest one, in two different habitats (the Kampinos Forest and Dzika Jabłoń Island in the Masurian region) for several years. These show mostly skewed distributions with skewness coefficients greater than zero. However, the samples consisted of individuals differing by age. To eliminate the effect of age, frequency distributions were calculated only for the males that had a high probability of being born and reaching the age when they could be trapped, during the period between two successive sampling occasions, that is during a month and half. Their distributions were negatively skewed and J-shaped. On the next sampling, however, the weights of these individuals had a positively skewed distribution. The usefulness of these results for the present considerations is limited because the males can only be trapped when they are 21 days old or older, and they were caught at six-week intervals. This means that the frequency distributions of their weights included individuals differing in age by more than ten days. During such a period the weight of bank voles can increase by a dozen or so grams, which represents a high percentage of their maximum body weight. When calculating the growth curve of the bank vole, the author found that the standard deviation, and, when it could be calculated, the variability coefficient, increased with age.

Recently Markowski (1980) provided rich data on the morphometric variability in the northern vole *Microtus oeconomus*. However, the frequency distributions of individual weights for animals caught in successive months in 1966 are useless here because of differences in age and complexity of ecological interactions in the population under study. It is possible however, that the sample taken in December, which is characterized by a slight positive skewness, was more uniform with respect to age than the other samples, as some other data in this paper show that in this month only the individuals born in the current year can be present in the population. A similar situation is present in the case of abundant materials collected by Adamczewska-Andrzejewska (1959) for frequency distribution of individual weights in the field mouse *Apodemus flavicollis* and the striped field mouse *Apodemus agrarius* (Adamczewska-Andrzejewska 1973).

Fox & Kemper (1982) carried out laboratory experiments on the growth and development of the rodent *Pseudomys gracilicaudatus*. The growth curves presented by these authors not only include information about changes in the average weight, but also show that the dispersion of individual weights about the average value increases with age (figure 22). However, the existing data did not enable us to correlate the increase in differentiation of weight with the conditions of growth.

Murton *et al.* (1966), who studied regulatory factors in the population of wood pigeons

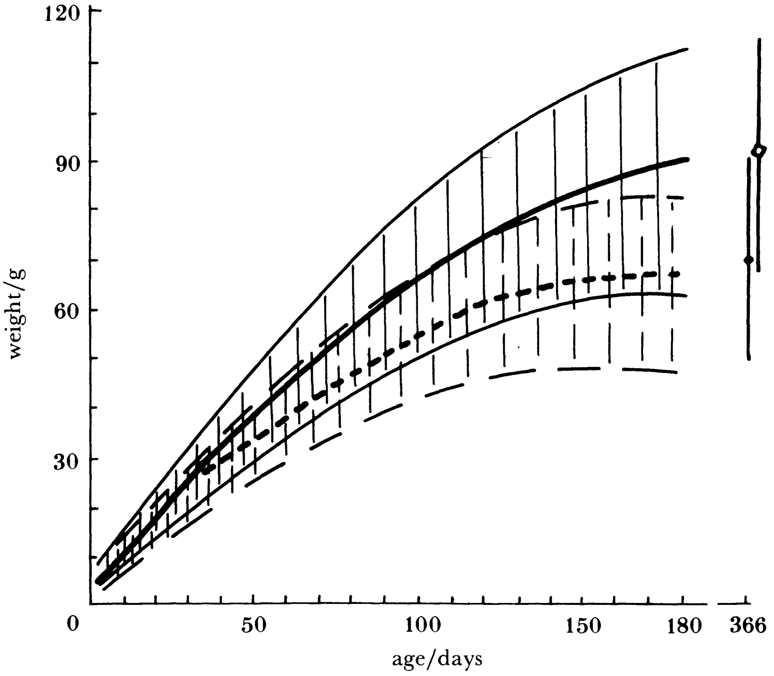

FIGURE 22. Growth curves of *Pseudomys gracilicaudatus* males (——) and females (— —). Changes of average body weight are indicated together with 95% confidence limits. (Redrawn from Fox & Kemper (1982).)

*Columba palumbus*, examined frequency distributions of individual weights for adult and juvenile birds trapped or shot. These data are difficult to interpret because of differences in mortality and in ability to be trapped for individuals of different age and size. The frequency distributions were both positive and negative, and there were also symmetric distributions. The positively skewed frequency distributions, calculated for different years and months (January, February, March) were more frequently recorded for young birds. From January to March, the skewness coefficient of weight distribution increased for both young and adult, though it could be less than zero all the time. Also a relationship was observed between the shape of weight distribution for adults and the density of clover on different sites. The distribution was symmetric on the richest site and positively skewed on the poorest site.

There are relatively rich data on the differentiation and size distribution in insects. The results of the study carried out by Ciesielska (1966) on the ecology of a store pest *Oryzaephilus surinamensis* are particularly clear (figure 23). Independent experiments were conducted on food preference in this species. It had been found that there was a range of preferred food items. The frequency distribution of individual imago lengths was calculated for insects reared on different diets. After the first month the length distribution for the animals kept on a diet of preferred food approached a symmetric curve with a slight tendency towards negative skewness, while the curve was positively skewed for insects supplied with the least preferred food. In all cases of intermediate diet, the frequency distributions were irregular after the first month, but with a predominance of positive skewness. After two months of the experiment only the insects supplied with the most preferred food maintained an unchanged frequency distribution for their lengths, while in the other cases positive skewness was more pronounced, particularly on the diet of least preferred food. This was coupled with relatively smaller increases in mean body

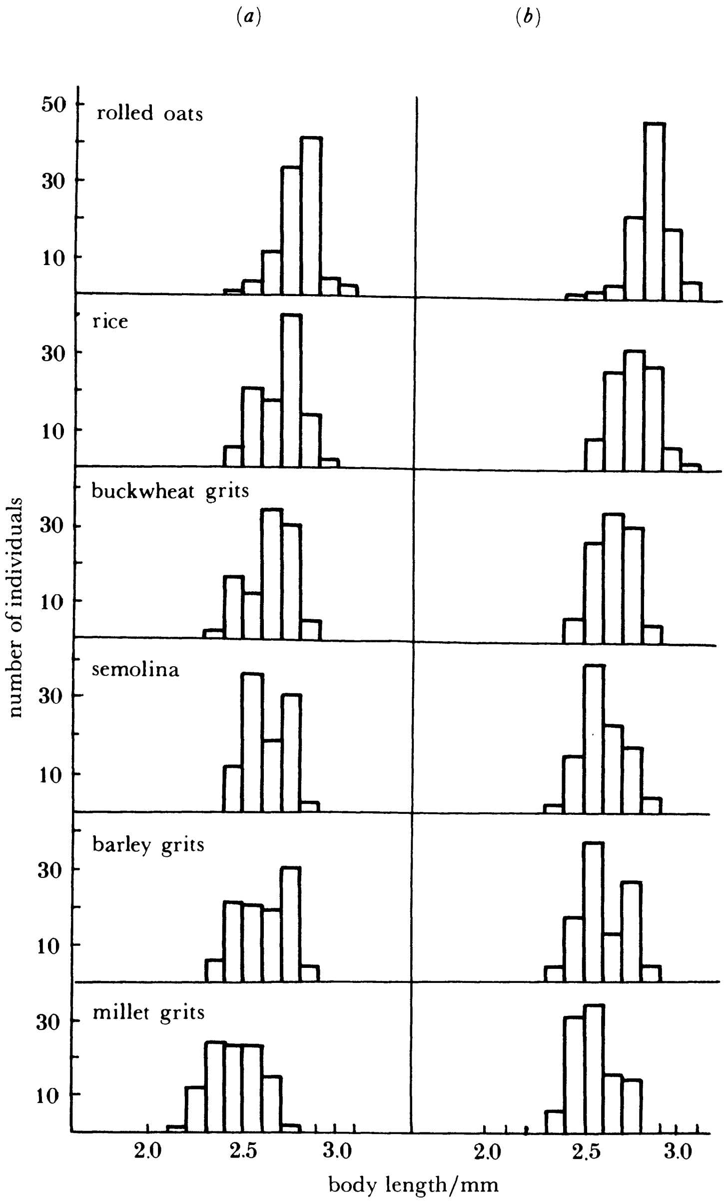

FIGURE 23. Frequency distributions of body length for *Oryzaephilus surinamensis* imagos cultured on different food. (*a*) After one month of culture; (*b*) after two months of culture. Food conditions are deteriorating from top to bottom. (Redrawn from Ciesielska (1966).)

weights under poorer food conditions. After the first month, differences were observed in standard deviation and in the variability coefficient of length distributions. Both were higher for insects supplied with poorer food, and this correlated with the gradient of declining food preference. After two months of the experiment, the general picture was the same with only one difference: the differences in standard deviation and variability coefficient between cultures with best and poorest food conditions were lower than a month earlier, which was due to an increase in mortality under poor trophic conditions.

Recently, Skinner (1980) examined frequency distributions of body weights for foraging ants

*Formica rufa*. They were positively skewed, though the only indication that this group of ants is even-aged is a general view that in social insects activity type is age-related.

Axelsson *at al.* (1973) have found that the frequency distributions of individual weights in *Coleoptera* populations are positively skewed, and Persson & Lohm (1977) recorded positive skewness in *Collembola*.

Elliott (1973) studied the life cycle and size structure in a population of the leech *Erpobdella octoculata*. One generation of this species lived two years in the study area. The first young individuals appeared in August–September. Their growth was relatively slow by March of the following year, very rapid between March and July–August, and slow again by September–October. They became sexually mature at the end of the second year of life. The changes in the number of individuals in particular size-classes and the changes in mean body weight for five successive generations imply that the frequency distributions of individual weights were positively skewed by the end of the period of rapid growth, and that then they developed negative skewness or were symmetric. Positively skewed distributions occurred at relatively high and stable densities, while symmetric and negatively skewed distributions occurred during periods of drastic declines in density. Elliott fitted exponential functions to the curves of growth during these characteristic periods and showed that the confidence intervals for these regressions, which are correlated with the variability in weight, increased with age.

There are some data indicating that in *Enchytraeidae* populations the skewness coefficient of weight distributions is greater than zero (Nielsen 1961). It is probable, however, that the samples used for this analysis consisted of individuals differing by age. Similar results were also obtained for *Lumbricidae* (Satchell 1971).

## 4. Summing-up and interpretations of experimental data

The individual weight, as a character controlled by many genes, should have a normal distribution in even-aged populations (Maynard Smith 1958). But the experimental data discussed in the preceding sections show that this is not the case. The conclusions from the two preceding sections can be summarized as follows.

(1) The frequency distributions of individual weights for even-aged plant and animal populations are most often positively skewed. This means that there are two types of frequency distribution shapes. One, the so-called L-shaped frequency distribution, is characterized by an increase in frequency or number of individuals towards the class of the smallest individuals. In the other type, one of the intermediate weight classes is most frequent, but the mode is shifted to the left relative to the average weight, to maintain a coefficient of skewness greater than zero. However, symmetric and negatively skewed weight distributions are also observed in both laboratory cultures and natural populations.

(2) Symmetric distributions, or less often negatively skewed distributions, are characteristic of even-aged populations of organisms starting their individual development.

(3) Skewness of weight distribution in even-aged populations varies with individual growth, independent of the initial shape of the distribution. Two kinds of changes in shape can be distinguished. In the case of experimental cultures the initially symmetric distributions develop a positive skewness increasing with time. Therefore, an increase in skewness coefficient can be observed between any time instants and not just between the original and a given time instant. 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. It should be noted, however, that skewness does not always increase with time, even in the first period of growth. In some situations it can be stable or even decreasing.

(4) The rate at which frequency distributions of individual weights develop, increasing positive skewness and the degree of skewness obtained, largely depends on the population density and on 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 coefficients. Environmental pollution also accounts for a skewness increase.

(5) It is observed, at least in plant populations, that high mortality is related to an early development of skewness in weight distributions, or to a high value of the skewness coefficient. In the case when weight distribution remains symmetric, mortality is lower.

(6) 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, the data available being scarce compared with those concerning skewness. In cases when some patterns are observed, however, most often the variance or variability coefficient increases with individual growth in the population, as with skewness.

(7) Where some patterns can be recognized, an increase in the density of even-aged populations or deterioration of food conditions, for example, a decrease in the quality, concentration or availability of food, account for an increase in weight variability in the population.

The first attempts at describing mechanisms generating skewed distributions in Nature go back to the beginning of this century. For example, in 1903 J. C. Kapteyn published a book entitled *Skew frequency curves in biology and statistics*. The so-called Kapteyn's theory of proportional effect (quoted after Attchison & Brown 1957) describes how to generate a log-normal distribution, which is a skewed frequency distribution with a skewness coefficient greater than zero. For our purposes, this theory can be presented as follows. Let us describe the growth of an individual in discrete time units. Let $w^i$ be the body weight at time instant $i$, where $i = 1, \ldots$. The law of proportional effect shows that the increase in weight between two successive time instants equals a randomly selected weight fraction in the earlier of these two time instants. This means that

$$w^i - w^{i-1} = \epsilon^i w^{i-1}, \tag{4.1}$$

where $\epsilon^i$ is a randomly selected number of the set $\{\epsilon^i\}$, the values of $\epsilon^i$ are independent of each other and they do not depend on the body weight, and $0 < \epsilon^i < 1$. In this model the frequency distribution of individual weights will be log-normal for sufficiently large values of $i$.

The law of proportional effect is not sufficient to explain the observed patterns. It can be used as a theoretical background at point (1), since it explains how to construct a distribution with a skewness coefficient greater than zero. But the biological interpretation of this law gives rise to objections because it requires an assumption that the randomly selected fraction of the weight incorporated into tissues of the growing organism does not depend on the weight increments in earlier time steps, nor on the weight itself. This assumption seems sophisticated when growth processes are described. The law of proportional effect does not consider the relationships described at points (4) and (7). It would be possible, however, to include the effect of density and environmental conditions on skewness assuming that the variance of the frequency distribution of $\epsilon^i$ increases with growing density or deteriorating habitat conditions. From the properties of the log-normal distribution (Attchinson & Brown 1957), this would increase the skewness coefficient of weight distribution, and this would give rise to new difficulties in the biological interpretation of this assumption.

Further attempts to explain the properties of weight distribution were made in the second half of the 1950s, when Japanese scientists did experiments on frequency distributions of individual plant weights, and also tried to interpret their observations. Koyama & Kira (1956) assumed that the growth of plant weight follows an exponential equation of the form

$$\mathrm{d}w/\mathrm{d}t = r'w, \tag{4.2}$$

where the relative growth rate, $r'$, is a constant characteristic of a plant. Thus,

$$w(t) = w_0\,\mathrm{e}^{r'(t-t_0)}, \tag{4.3}$$

where $w_0$ is the initial weight of the plant at the initial time instant $t_0$. Then the authors assumed that the population consisted of $N$ such plants, each of them growing exponentially. If we assume that the relative growth rate, $r'$, is constant and the initial weights, $w_0$, have a normal distribution in the population, then the weight distribution at any later time instant will be normal, with a constant variability coefficient and a variance increasing exponentially. If we made the opposite assumption, that is, that the initial body weight in the population is constant, and the relative growth rate has a normal distribution, then, on taking the logarithm of both sides of (4.3) we get

$$\ln w = \ln w_0 + r't. \tag{4.4}$$

Since $w_0$ is constant and $r'$ has a normal distribution, then $\ln w$ also has a normal distribution. Therefore, the body weight has a log-normal distribution. This is a version of Kapteyn's scheme.

The calculations show that in this model the skewness coefficient increased with time, and the distributions were finally L-shaped (figure 24). Koyama & Kira (1956) also analysed the

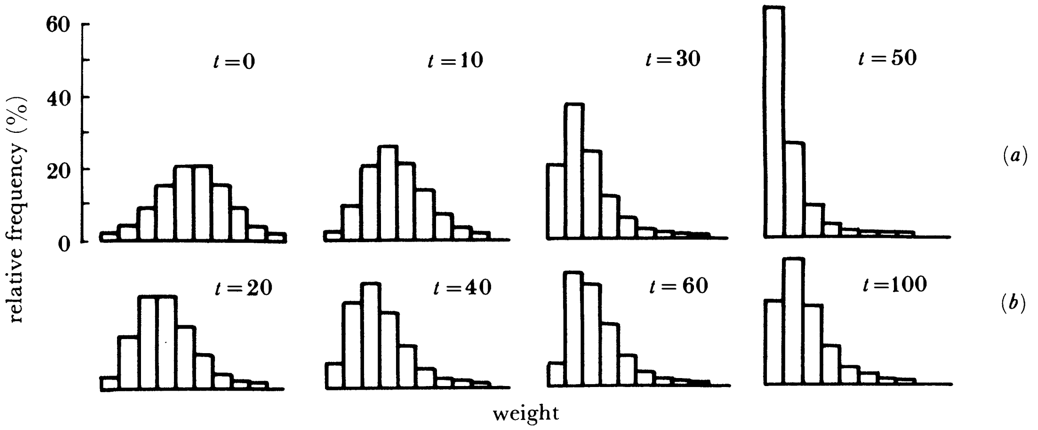

FIGURE 24. Frequency distributions of individual weights obtained by Koyama & Kira (1956) in simulations. Changes of these distributions over time are shown: (a) model with constant initial weight $w_0$ and relative growth rate $r'$ taken from normal distribution. These variables were randomly combined once at the beginning of the simulation; (b) $w_0$ and $r'$ were successively randomly combined every ten time steps of simulation. (Redrawn from Koyama & Kira (1956).)

situation where both the initial body weight, $w_0$, and the constant, $r'$, had normal distributions, and they presented numerical examples of weight distributions for some selected distributions of $w_0$ and $r'$. In all the cases the skewness coefficient was greater than zero, and increased with time, this process being more rapid when the variance of the frequency distribution of relative growth rate, $r'$, was greater. The value of the mean of the frequency distribution of growth rates had a significantly less important effect on the development of skewness for weight distribution. Even non-random pairing of $r'$ and $w_0$ did not accelerate this process. No differences were recorded when large values of $w_0$ were coupled with a large value of $r'$. Skewness appeared much earlier when $r'$ and $w_0$ were paired only once at the beginning of the simulation and not at each time step.

These considerations inclined Koyama & Kira (1956) to state that 'the transition from the normal to the L-shaped frequency curve is the natural outcome of the exponential nature of plant growth as well as variability of relative growth rate, presumably of the Gaussian type'. As the models for differentiation of body weights did not assume interactions among plants, the authors conclude that skewed weight distributions should also be expected for plants growing in isolation, provided the growth is exponential and the relative growth rate has a normal distribution. This last assumption, as Koyama & Kira acknowledge, is poorly documented. Although competitive interactions are not the most important factor responsible for skew distribution, they may accelerate the appearance of skewness and exaggerate it. As the authors suggest, this may be shown through an increase in the variance of the frequency distribution of relative growth rate when competitive interactions occur. After a sufficiently long time, each frequency distribution of weights in the population with or without competitive interactions become L-shaped. The lightest individuals are most common and there is a relatively small number of heavy individuals. The time until this situation is reached is very variable, however, and in some situations even longer than the growing season, which, together with a lack of interactions among individuals, can account for a continued presence of symmetric distributions of weights throughout the experiment.

Similar implications can be found in Koch (1966, 1969). He stated that the body weight is a variable which can be obtained by multiplying three linear dimensions of an organism. The author proves that the product of $n$ variables will approximate the log-normal distribution, independent of whether they are correlated or not. This log-normal approximation improves with increasing number of variables multiplied. The interpretation of these statements is consistent with Koyama & Kira's findings: a positive skewness of weight distribution need not be a result of interactions among individuals, but it may develop as an intrinsic consequence of growth.

I know two papers in which a model of the differentiation of body size was developed as a side result of considering other subjects. DeAngelis *et al.* (1980), already quoted here, studied the effect of cannibalism on the distribution of weights in the largemouth bass population. An increase in the weight of fish $i$, which eats the $j$th fish and $R$ weight units of alternative food, mostly *Daphnia* per unit time, is

$$\Delta w_i = \alpha_2(w_j + R_i), \tag{4.5}$$

where $\alpha_2$ is the biomass conversion efficiency coefficient. It is assumed that the daily consumption of *Daphnia*, $R_i$, is a power function of fish weight, and that the probability of consumption of the $j$th fish by fish $i$ depends on the ratio of their body lengths. Another power function was used to convert from length to weight. In these assumptions, the weight distribution in the model population was positively skewed in both cases, that is with alternative *Daphnia* food available and when the fish was the only food available.

Beyer & Laurence (1980) also described, in the paper already quoted, growth and size structure in a population of fish larvae. They assume that the weight $w_{i+1}$ of a larvae at time $i+1$ depends on the weight $w_i$ at time $i$ according to the formula

$$w_{i+1} = w_i + 0.56\,R_i^w - 1.1\,w_i^{0.74}, \tag{4.6}$$

where $R_i^w$ is food ration of the larva of weight $w$ at time $i$, 0.56 is a food conversion efficiency, and the term $1.1\,w_i^{0.74}$ represents respiratory losses. Probability $P(R^w = x)$ that the food ration of a larva of weight $w$ will be equal to $x$ was found from the Poisson distribution

$$P(R^w = x) = [(R_m^w)^x/x!]\ \mathrm{e}^{-R_m^w}, \tag{4.7}$$

where $R_m^w$ is the mean food ration of a larva of weight $w$. On the basis of the known empirical relationship between the length and weight of larvae, speed of their movement, and some assumptions concerning the capability of prey recognition, it was assumed that

$$R_m^w = v\,3.5\,w^{0.8}, \tag{4.8}$$

where $v$ is food density.

An analysis of the distribution (4.7) shows that the range of food rations with probabilities significantly greater than zero is much larger for heavy than for light larvae, and also, as (4.8) shows, the mean food ration is greater for heavy larvae. However, the probabilities of changes in weight on these food rations are much less than for light individuals, for which the range of food ration is narrow, mean food ration small, but the probability of change in weight high. The authors imposed some limitations on the maximum and minimum food ration. The mean food ration of a larva of weight $w_i$ could not be greater than $2.0\,w_i^{0.81}$ and smaller than $1.96\,w_i^{0.74} - 0.18\,w_i$. The first restriction results from additional assumptions on the volume of the alimentary canal and the time of food digestion, and the second one corresponds to a mean daily weight loss of 10%. The model also included a mechanism eliminating individuals from the population if the growth curve in a given time unit was steeper than the exponential curve corresponding to a 3% daily weight increase.

In final calculations, the distribution (4.7) was replaced by the corresponding normal distribution, because the increase in the mean food ration was very rapid and at high mean values the Poisson distribution approximates the normal distribution. None the less, this complicated model generated positively skewed frequency distributions of larval weights. The skewness coefficient increased with time. Finally, after 42 days of simulation, the weight distribution became L-shaped. Unfortunately, the effect of food density on the development of frequency distributions is not described. But (4.7) and (4.8) imply that a decrease in food density leads, through a decrease in the mean food ration, towards a decreasing in the range of food rations and an increase in the probability of catching a mean food ration.

Recently Łomnicki (1980*b*) presented a simple model for generating weight distributions, to illustrate the development of differentiation among members of even-aged populations. He has assumed that the population consists of $N$ individuals and that $V$ identical food particles are available in the habitat. The probability $P$ of taking a food particle and incorporating it into body tissues was related to the actual weight, $w$, of an organism and actual number, $V$, of food particles according to the formula

$$P(w, V) = 1 - e^{-c'wV}, \tag{4.9}$$

where $c'$ is a constant. Equation (4.9) says that the probability of taking a food particle when the number of particles in the environment is constant is greater for heavier individuals. It also increases with growing amount of food. Such a growth of individuals in the population was simulated for certain assumed initial food supply rates and with the initial body weight identical for all individuals. At the end of the simulation the frequency distributions of weights were positively skewed. The mean weight and the skewness coefficient increased in the first period, then stabilized at a certain level. At the end of simulation the individual body weight was highly correlated with weights in preceding time units. This means that the rank of an individual in the size hierarchy becomes established in the first steps of simulation, and it remains unchanged throughout subsequent growth stages: larger individuals have greater weight increases.

There are fundamental differences between the model proposed by Kapteyn and further developed by the Japanese workers, and those later developed by DeAngelis *et al.* (1980) Beyer & Laurence (1980) and by Łomnicki (1980*b*) The biological interpretation of the models of the first group is unsatisfactory. The models of the second group are more realistic as they consider the growth rate in relation to the weight itself, they include a description of the food ration, the effect of food availability on food ration, and respiratory losses. These models, except for a very simplified Łomnicki's model, are only relevant to a strictly determined ecological situation and to a single, particular species. The first group of models assumes a random distribution of growth parameters for population members, while the second group assumes a relation between the chance of getting successive food rations and the amount of food already consumed. What these two groups have in common is that they are either stochastic models or deterministic models with random parameters. In an enormous predominance of deterministic growth models over stochastic ones this can only be explained by the fact that by using stochastic models it is 'easy' to obtain skewed distributions of weights.

It seems that the facts concerning the differentiation and frequency distributions of individual weights in even-aged plant and animal populations described in §§2, 3 and 4 can be explained in the way presented below: I will try to prove these theses in the subsequent sections.

(8) Resources are unevenly partitioned among members of even-aged populations. The individual resource intake depends on the intake in the past, on the abundance of this resource in the environment, and on the presence of other individuals in the population. Differences in resource intake increase when the resource is scarce and vanish when it is in excess.

(9) Unevenness in the partitioning of resources accounts for the differentiation of weights and the development of positively skewed weight distribution during growth. An increase in the population density or a decrease in the environmental resources, or both, lead, through changes in the partitioning of resources among population members, towards an increasing skewness of weight distributions and increasing weight differentiation. The opposite situation, that is, a decrease in population density or an increase in the amount of resources, or both, result in decreased skewness and differentiation. At a low density and optimum resource supply in the environment, the body weights become uniform. This pattern should be independent of the initial frequency distribution of weights.

It should be possible to describe the pattern presented at point (9) and resulting from assumptions noted at point (8), by using both stochastic and deterministic models of growth, as these two approaches are equally valid for the development of growth models.

Let us note that the concept presented here is totally different from that proposed by Koyama & Kira (1956). It is not assumed that skewed frequency distributions are an intrinsic feature of growth processes, while individual interactions are of secondary importance. On the contrary, in this paper I shall try to provide evidence that skewed distributions are developed as a consequence of competition for limited and unevenly partitioned resources, with emphasis on the significant effect of environmental conditions for growth.

## 5. DIFFERENTIATION AND FREQUENCY DISTRIBUTIONS OF BODY WEIGHTS IN CLASSIC DETERMINISTIC GROWTH EQUATIONS

Let us examine the possibility of using the classic, deterministic growth equations to describe the differentiation of body weights in even-aged populations. The general, classic, deterministic growth equation can be written in the form

$$\mathrm{d}w/\mathrm{d}t = G(w), \tag{5.1}$$

where, for example, $G(w) = r'w$ in the exponential growth equation, $G(w) = Hw^m - Kw$ for the Bertalanffy and Winberg equations, and $G(w) = a_1 w^{b_1} - a_2 w^{b_2}$ for the balance equation (see Appendix 2).

Let us consider first the case of limited growth. Then the equation

$$G(w) = 0 \tag{5.2}$$

has $n$ positive solutions, $w^j_\infty, j = 1, \ldots, n$, where $n \geqslant 1$. Let us assume that $n = 1$. This is the case for the Bertalanffy, Winberg and balance equations. Equation (5.2) has only one solution, $w^1_\infty$. It follows from biological assumptions that

$$w_0 < w^1_\infty, \tag{5.3}$$

where $w_0$ is the initial weight in (5.1) as this equation describes actual growth. In this situation, independent of the initial weight, the weight will converge to $w^1_\infty$

$$\lim_{t\to\infty} w(t) = w^1_\infty. \tag{5.4}$$

This means that the weights gradually become equal.

Let us assume, in turn, that $n > 1$. Then equation (5.2) has $n$ different solutions, which are equilibrium points of growth equation (5.1). Some of them are stable, which means that, dependent on the initial weight, the individual weights will converge to any of these stable points with time. In the situation when the difference between solutions to equation (5.4), which at the same time are the stable points of equation (5.1), is greater than differences between the corresponding initial weights, after a sufficiently long period of time we will get an increase in weight differentiation.

Now let us consider the case of unlimited growth. The following inequality must be satisfied for the growth

$$G(w) > 0 \tag{5.5}$$

for $w > 0$, and (5.2) cannot have positive solutions. The exponential growth equation can be used here as an example. Let us consider two individuals of body weights $w_1(t)$ and $w_2(t)$ at time $t$. Then

$$\Delta w(t) = w_1(t) - w_2(t) \tag{5.6}$$

and

$$\mathrm{d}\Delta w(t)/\mathrm{d}t = \{\mathrm{d}w_1(t)/\mathrm{d}t\} - \{\mathrm{d}w_2(t)/\mathrm{d}t\} = G(w_1(t)) - G(w_2(t)) \approx \{\mathrm{d}G(w_2(t))/\mathrm{d}w\}\,\Delta w(t). \tag{5.7}$$

Thus the increase in differences between body weights depends on the sign of the derivative $\mathrm{d}G/\mathrm{d}w$. The differences increase when this derivative is positive, that is, when the heavier individual gains more weight per unit time than the lighter one, as is the case in the equation of exponential growth.

It can be stated, therefore, that the classic, deterministic growth equations most frequently describe the unification of weights, when these are equations of limited growth (the Bertalanffy, Winberg and balance equations). This process always occurs after a sufficiently long time period. In the case of an abstract growth equation with $n$ solutions to (5.2) (abstract because for all classic equations $n = 1$) the distribution of final weights has an artificial character: it is represented by some number of isolated peaks corresponding to stable equilibrium points of (5.1), although the differences in final weights may be greater than initially. The most common version of the unlimited growth equation, that of exponential growth, describes permanent differentiation of weights during growth. It follows from Appendix 2 that exponential growth does not change the shape of weight distribution. If at the initial time instant the weight distribution is symmetric, it will remain symmetric at later time instances, provided the organisms are growing exponentially. Thus it can be seen that the classic, deterministic growth equations cannot describe the properties of weight distributions that are presented in the preceding section. Weight differentiation in deterministic, classic growth equations is discussed in detail in Appendix 2.

The situation becomes a little more complicated for some specific growth equations such as Robertson and Ostwald, Gompertz, Schmalhausen and Zotin's equations (see Majkowski & Uchmański 1980), which are not autonomous equations, that is when $G = G(w, t)$. It means that an increase in weight per unit time depends not only on weight but also on time or age of an organism. However, owing to limited usefulness of these growth equations in biology, we will not discuss them now.

## 6. A DETERMINISTIC MODEL FOR DIFFERENTIATION OF BODY WEIGHTS: THE CASE WITH A CONSTANT FOOD SUPPLY

### 6.1. *Formulation of the model*

Let us consider an even-aged population of $N$ individuals. Assume that each individual in this population is characterized by an initial body weight $w_0$. We can construct the frequency distribution of initial weights in the population and determine the mean, variance and skewness coefficient of this distribution. In addition, let us accept one of the assumptions below.

(1) Let the habitat consists of $m'$ ($m' \geqslant N$) areas differing in food concentration or availability. If $V$ denotes an average food concentration or availability in the habitat, then in the $i$th area the food concentration or availability equals to $\epsilon_i V$, where $\epsilon_i$ is a certain number close to one

(figure 25). At the initial time $t_0$ these areas are colonized by the population of even-aged individuals, the better area (with greater $\epsilon_i$) being occupied by an individual with a higher initial weight.

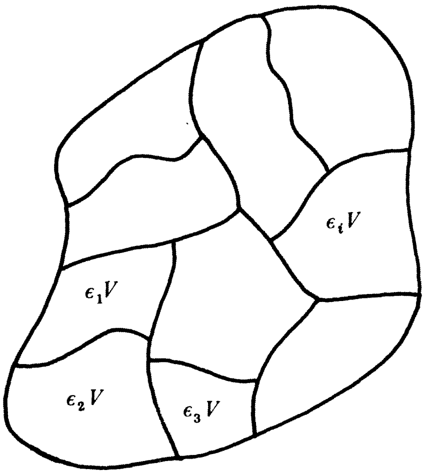

FIGURE 25. Division of the space into subareas with different availability or concentration of resources. It allows differentiation of body weights during growth.

(2) The habitat is homogeneous, but the size of area occupied by an individual at the initial time instant will depend on the initial weight of this individual.

The colonization of an area can be described literally as settling in a physical space with different trophic conditions, and also as other ways of the distribution of individuals in different ecological spaces, for example, the development of seedlings with diversified root systems in the case of plant populations.

As experimental results show (see for example, Sushchenya & Khmeleva 1967; Sushchenya 1975, for crustaceans) individual consumption, $C$, in many cases is a power function of body weight

$$C = a_1' w^{b_1}. \tag{6.1}$$

It also depends on the amount of food available, in such a way that in (6.1) only parameter $a_1'$ varies in relation to food availability ($b_1$ is a constant). The Ivlev function (Ivlev 1955) can be used to describe this relation in the form

$$a_1' = a_1''(1-e^{-\alpha_1 V}), \tag{6.2}$$

where $V$ is the amount of food available, while $a_1''$ and $\alpha_1$ are constants. Note that a power function similar to (6.1) can be used to describe the relation between assimilation rate and the body weight of an animal, provided the coefficient of assimilation efficiency is constant.

Consumption or assimilation in animals has its equivalent for plants. The relation between assimilation and the weight of plants is discussed by Ledig (1969) and Thornley (1976). The assumption of a power relationship between assimilation and weight seems to be valid also for plants (Richards 1959; for discussion see Żelawski & Sztencel (1981)). It is also expected that the increase in plant weight will depend in a similar way on the amount of nutrients available in the soil.

Assumptions (1) and (2) imply that particular individuals of the even-aged population grow under diverse trophic conditions, in a habitat which on the microscale is heterogeneous with respect to trophic conditions for individual organisms. On the one hand, there should be a relation between assimilation and the mean food concentration or availability in the habitat. On the other hand, we should take into account the previously noted heterogeneity in food concentration or availability, which, as assumed at points (1) and (2), are correlated with the initial weight of an individual. According to this, the assimilation will be proportional to

$$a_1\,y(w_0,\,V)\,w^{b_1}, \tag{6.3}$$

where $a_1$ is a constant coefficient, while $y(w_0, V)$ is a general function of the initial body weight and mean food concentration in the habitat.

The same result is achieved if we replace assumptions (1) and (2) with the following one.

(3) There is a physiological relation between the initial weight and the rate of weight assimilation, although growth occurs in a homogeneous habitat from the point of view of each individual.

For the purpose of the present paper there is no need to look for a specific form of the function $y(w_0, V)$. This assumption should be satisfied for this function to have a good biological interpretation. Let us make the following assumptions for this purpose (figure 26).

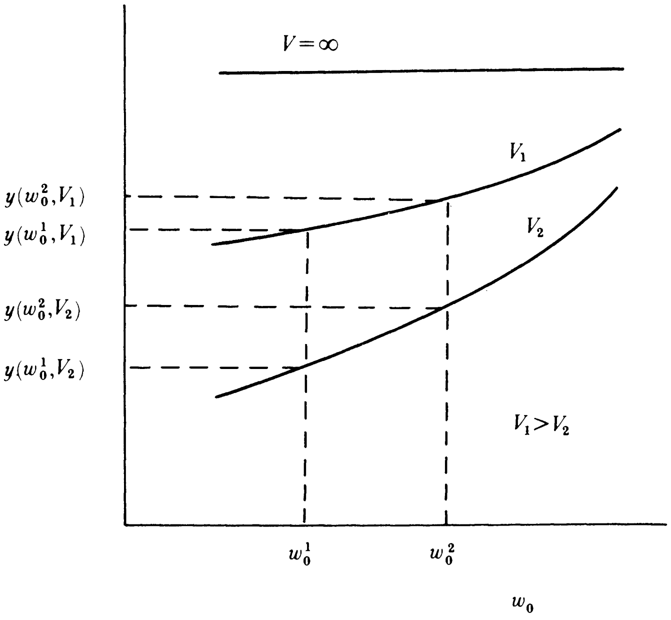

FIGURE 26. Theoretical shape of function $y(w_0, V)$ describing resource partitioning among individuals in a deterministic model of weight differentiation. Assumptions concerning dependence on resource availability or concentration and initial weight are illustrated.

(4) Of two individuals with equal body weights under constant, though not optimal, food conditions the individual with greater initial weight will have greater assimilation rate. Mathematically we can say that function $y(w_0, V)$ at a constant food supply $V$ is a non-decreasing function of the initial weight

$$\partial y(w_0,\,V)/\partial w_0 \geqslant 0. \tag{6.4}$$

(5) Assimilation of an individual is greater under better trophic conditions. In other words, function $y(w_0, V)$ is, at a constant initial weight, an increasing function of food supply

$$\partial y(w_0, V)/\partial V > 0. \tag{6.5}$$

(6) Under optimum food conditions, that is, on the assumption that food is unlimited ($V = \infty$), assimilation is a power function of the actual weight, and it does not depend on the initial weight. This means that

$$y(w_0, V)\,|_{V=\infty} = a, \tag{6.6}$$

where $a$ is a constant.

(7) An improvement in food conditions is followed by a decrease in differentiation of assimilation. In other words, the derivative $\partial y(w_0, V)/\partial w_0$ decreases with increasing $V$, or for $V_1 < V_2$ an inequality

$$\left.\frac{\partial y(w_0, V)}{\partial w_0}\right|_{V=V_2} < \left.\frac{\partial y(w_0, V)}{\partial w_0}\right|_{V=V_1} \tag{6.7}$$

is satisfied.

(8) A decrease in the amount of food available in the habitat causes a greater decrease in assimilation for individuals with smaller initial body weights, compared with those with greater initial weights. This means that for each pair of $w_0^1$ and $w_0^2$ such that $w_0^1 < w_0^2$ we have

$$\left.\frac{\partial y(w_0, V)}{\partial V}\right|_{w_0=w_0^1} > \left.\frac{\partial y(w_0, V)}{\partial V}\right|_{w_0=w_0^2}. \tag{6.8}$$

Let us note that assumptions (7) and (8) can be reduced to one assumption

$$\frac{\partial^2 y(w_0, V)}{\partial V \partial w_0} = \frac{\partial^2 y(w_0, V)}{\partial w_0 \partial V} < 0. \tag{6.9}$$

Let us assume that the rate of respiration $R$ is also a power function of weight (Duncan & Klekowski 1975), and it does not depend on the initial weight and on the amount of food in the habitat

$$R = a_2 w^{b_2}, \tag{6.10}$$

where $a_2$ and $b_2$ are constants. Relationship (6.10) is supported by many experiments done with animals (Duncan & Klekowski 1975) and with some restrictions it seems to be valid also for plants (Richards 1959). Assimilation is described by (6.3). In the periods when only somatic production occurs, for example, before maturity is reached, the rate of weight growth can be described by

$$\mathrm{d}w/\mathrm{d}t = a_1 y(w_0, V)\, w^{b_1} - a_2 w^{b_2}. \tag{6.11}$$

To secure real growth, it should be assumed that $b_2 > b_1$. In reality, $b_2$ is most often greater than 2/3. To simplify the calculations, let us assume that the exponent $b_2$ is close to one. Then, (6.11) will take the form

$$\mathrm{d}w/\mathrm{d}t = a_1 y(w_0, V)\, w^{b_1} - a_2 w. \tag{6.12}$$

This equation, with the accuracy of the factor depending on the initial body weight and amount of food, resembles the Bertalanffy equation used to describe growth in animals, but also in plants (Richards 1959; Żelawski & Sztencel 1981; McMurtie 1981). The solution to (6.12) is of the form

$$w(t) = \left\{\left[\frac{a_1}{a_2} y(w_0, V)\right] - \left[\frac{a_1}{a_2} y(w_0, V) - w_0^{1-b_1}\right] \mathrm{e}^{-a_2(1-b_1)(t-t_0)}\right\}^{1/(1-b_1)} \tag{6.13}$$

where $t_0$ is initial time. The solution (6.13) describes the asympotic growth following an **S**-shaped curve approaching the final weight $w_\infty$ given by the equation

$$w_\infty = [(a_1/a_2)\,y(w_0, V)]^{1/(1-b_1)}. \tag{6.14}$$

### 6.2. *Differentiation of body weights*

Let us consider two individuals with initial body weights $w_0$ and $w_0 + \Delta w_0$. Suppose that $\Delta w_0$ is small. Thus at initial time, $t_0$, the difference in weights equals to $\Delta w_0$. The value $\Delta w(t)$ of difference between weights at time $t > t_0$ is described by

$$\Delta w(t) = (\partial w(t)/\partial w_0)\,\Delta w_0. \tag{6.15}$$

When $\partial w(t)/\partial w_0 > 1$, the difference in weights increases with time. If this derivative is less than one, the difference in weights decreases, and when $\partial w(t)/\partial w_0 = 1$ the difference in weight does not change.

The differentiation of the right hand part of (6.13) with respect to the initial weight gives

$$\frac{\partial w(t)}{\partial w_0} = \frac{1}{1-b_1}\left\{\frac{a_1}{a_2}y(w_0, V) - \left[\frac{a_1}{a_2}y(w_0, V) - w_0^{1-b_1}\right]\mathrm{e}^{-a_2(1-b_1)(t-t_0)}\right\}^{b_1/(1-b_1)}$$
$$\times\left\{\frac{a_1}{a_2}\frac{\partial y}{\partial w_0} - \left[\frac{a_1}{a_2}\frac{\partial y}{\partial w_0} - (1-b_1)\,w_0^{-b_1}\right]\mathrm{e}^{-a_2(1-b_1)(t-t_0)}\right\}. \tag{6.16}$$

Substituting (6.16) into (6.15) we obtain an explicit form of the equation describing changes in differences between weights. Let us use the following symbols for factors on the right side of (6.16)

$$f_1 = \frac{1}{1-b_1}\left\{\frac{a_1}{a_2}y(w_0, V) - \left[\frac{a_1}{a_2}y(w_0, V) - w_0^{1-b_1}\right]\mathrm{e}^{-a_2(1-b_1)(t-t_0)}\right\}^{b_1/(1-b_1)} \tag{6.17}$$

and

$$f_2 = \frac{a_1}{a_2}\frac{\partial y}{\partial w_0} - \left(\frac{a_1}{a_2}\frac{\partial y}{\partial w_0} - (1-b_1)\,w_0^{-b_1}\right)\mathrm{e}^{-a_2(1-b_1)(t-t_0)}. \tag{6.18}$$

At $t = t_0$ the product of $f_1$ and $f_2$ is equal to 1. Equation (6.13) describes a strictly increasing function of time. It follows from this that function $f_1$ is also strictly increasing since the right side of (6.17) is proportional to the power $b_1$ of individual weight. Function $f_2$ will also strictly increase if

$$(a_1/a_2)\,\{\partial y(w_0, V)/\partial w_0\} - (1-b_1)\,w_0^{-b_1} > 0, \tag{6.19}$$

this being equivalent to

$$\partial y(w_0, V)/\partial w_0 > (1-b_1)\frac{a_2}{a_1}w_0^{-b_1}. \tag{6.20}$$

Therefore, when inequality (6.20) is satisfied, the product of functions $f_1$ and $f_2$ at $t = t_0$ is one, and at $t > t_0$ it is greater than one and increases with time. If inequality (6.20) is not satisfied, then the product of the increasing function $f_1$ and the decreasing function $f_2$ can change with time in two ways: it can decline with time, or it can increase first and then decrease to zero after reaching a maximum at a certain time instant (figure 27).

According to the earlier assumptions, the value of derivative $[\partial y(w_0, V)]/\partial w_0$ on the left side of inequality (6.20) at a constant food supply describes differences in the assimilation between individuals of different initial weights. These differences, and thus also the value of the

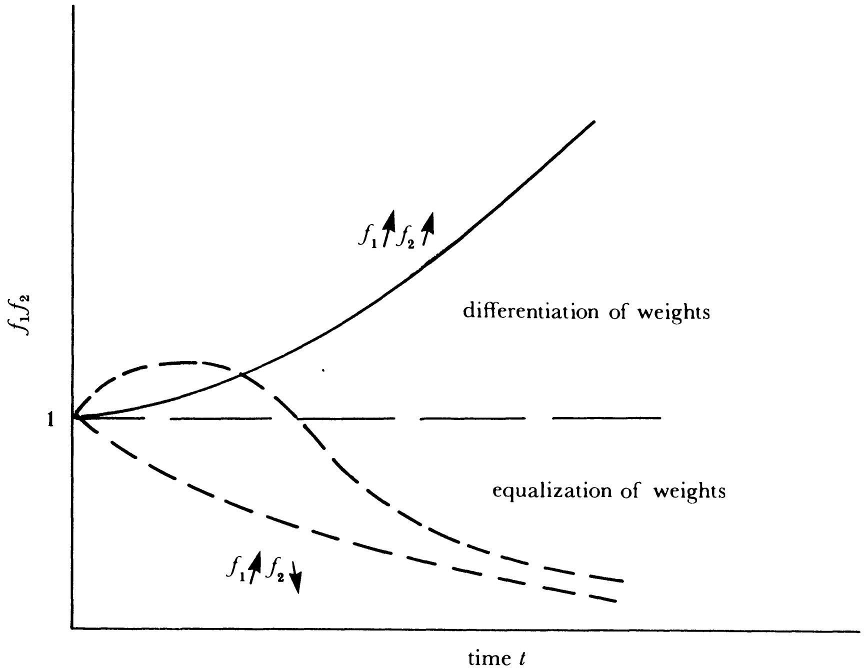

FIGURE 27. Time dependence of product of functions $f_1$ and $f_2$ in relation to various behaviours of these functions in separation. (For details see text.)

derivative, increase with declining food supply. Consequently, it can be assumed that there is a certain critical amount of food, below which the derivative takes a value satisfying inequality (6.20). As a result $\partial w(t)/\partial w_0$ in (6.15) become greater than one, and the differences in weights between individuals are increasing. When the food supply is greater than the critical value, then inequality (6.20) is not satisfied, and the model describes equalization of weights.

So far, differences in weights between paired individuals have been considered. For a population comprising $N$ individuals it is possible to satisfy inequality (6.20) for all $N$ individuals in sufficiently poor conditions because the derivative $[\partial y(w_0, V)]/\partial w_0$ is a decreasing function of the amount of food $V$; therefore we observe the differentiation in body weights for the whole population.

### 6.3. *Skewness of the frequency distribution of body weights*

We can determine skewness of a frequency distribution of weights by analysing the relation of differences in weights $\Delta w(t)$ to the initial weight. If at given time the difference $\Delta w(t)$ increases with increasing initial weight $w_0$, then the frequency distribution of weights will be positively skewed. Let us rewrite functions $f_1$ and $f_2$ in the form

$$f_1 = \frac{1}{1-b_1}\left(\frac{a_1}{a_2}y(w_0, V)\,(1-\mathrm{e}^{-a_2(1-b_1)\,(t-t_0)}) + w_0^{1-b_1}\,\mathrm{e}^{-a_2(1-b_1)\,(t-t_0)}\right)^{b_1/(1-b_1)} \tag{6.21}$$

$$f_2 = \frac{a_1}{a_2}\frac{\partial y}{\partial w_0}\,(1-\mathrm{e}^{-a_2(1-b_1)\,(t-t_0)}) + (1-b_1)\,w_0^{-b_1}\,\mathrm{e}^{-a_2(1-b_1)\,(t-t_0)}. \tag{6.22}$$

According to assumption (4) (§6.1), function $y(w_0, V)$, when $V$ is a constant and $V < \infty$, is an increasing function of $w_0$, similar to function $w_0^{1-b_1}$, because $b_1 < 1$. Thus function $f_1$ is an increasing function of the initial weight $w_0$.

The character of function $f_2$ cannot be determined in such a simple way. The second term in the equation of this function, which includes the term $w_0^{-b_1}$, is a decreasing function of the initial weight. The behaviour of the first term in relation to the initial body weight depends on the value of derivative $\partial y/\partial w_0$, which may be either a decreasing or an increasing function of the initial weight. Let us consider both these cases. An increase in the derivative $\partial y/\partial w_0$ with the initial weight implies that the differentiation in assimilation is greater among individuals of greater initial weights. A decrease in the value of derivative $\partial y/\partial w_0$ with increasing $w_0$ yields a higher differentiation in assimilation among individuals with smaller initial body weights (figure 28).

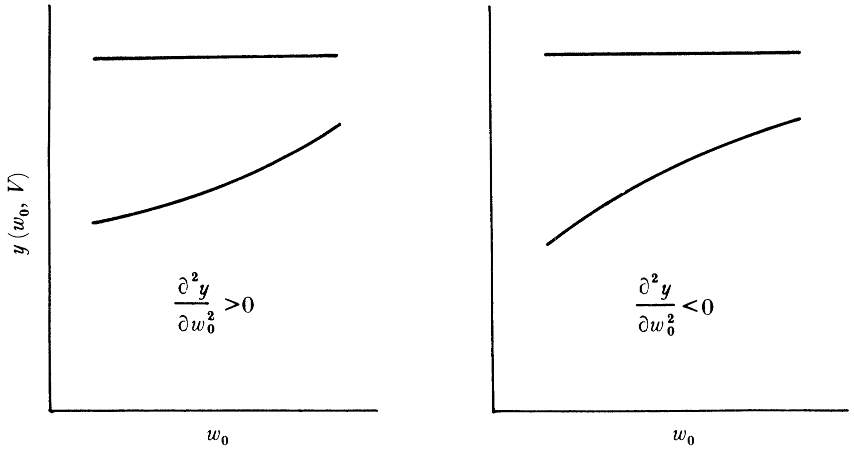

FIGURE 28. Two possible shapes of function $y(w_0, V)$; convex $\partial^2 y/\partial w_0^2 > 0$ and concave $\partial^2 y/\partial w_0^2 < 0$.

To simplify our analysis, let us consider a situation at the time instant when the exponential component of (6.21) and (6.22) is practically zero. Then

$$\lim_{t\to\infty} f_2 = \frac{a_1}{a_2}\frac{\partial y}{\partial w_0}. \tag{6.23}$$

Let the derivative $\partial y/\partial w_0$ be an increasing function of the initial weight. Then it follows from (6.23) that function $f_2$ is also an increasing function of the initial weight. The product $f_1 f_2$ is an increasing function of $w_0$ as well. Together with the assumption that inequality (6.20) is satisfied for all members of the population, this means that the increase in differences between body weights, $\Delta w(t)$, is greater for individuals with higher initial weights. As a result, this gives a positively skewed frequency distribution of weights at time $t$.

The situation becomes more complicated if $\partial y/\partial w_0$ is a decreasing function of the initial weight. Then the product $f_1 f_2$ is made up of an increasing function $f_1$ and a decreasing function $f_2$ of the variable $w_0$. In only some situations, which we cannot specify here without knowing the exact forms of functions $f_1$ and $f_2$, this product is an increasing function for a certain range of initial weights. Therefore, if the derivative $\partial y/\partial w_0$ is a decreasing function of the initial weights, the occurrence of a positively skewed weight distribution is not a rule.

We should now examine the relation between the shape of the weight frequency curve and the food supply. Let us assume that $\partial y/\partial w_0$ is an increasing function of the initial weight. Let us consider a pair of organisms with initial weights $w_0^1$ and $w_0^1 + \Delta w_0^1$ and another pair of organisms with initial weights $w_0^2$ and $w_0^2+\Delta w_0^2$, such that $w_0^1 < w_0^2$. The differences $\Delta w_0^1$ and $\Delta w_0^2$ are small. Let us assume again that we are describing the situation after a sufficiently long time for function $f_1$ to have its limit

$$\lim_{t\to\infty} f_1 = \frac{1}{1-b_1}\left(\frac{a_1}{a_2}y(w_0, V)\right)^{b_1/(1-b_1)}. \tag{6.24}$$

With these assumptions, and according to what was said earlier of the relation between function $y(w_0, V)$ and the initial weight, the following estimation is true:

$$f_1(w_0^1)f_2(w_0^1) < f_1(w_0^2)f_2(w_0^1) < f_1(w_0^2)f_2(w_0^2). \tag{6.25}$$

It follows from assumption (7) (§6.1) that a decrease in the amount of food available in the environment causes an increase in differences between the values of function $y(w_0, V)$ for different initial weights. Under deteriorating food conditions the differences in the values of function $f_1$ for $w_0^1$ and $w_0^2$ also increase (see (6.24)). In turn, it can be concluded from inequality (6.25) that even if the derivative $\partial y/\partial w_0$ took equal values at the two points (in reality it takes a higher value at point $w_0^2$), a decrease in the amount of food would be followed by an increase in differences between the products $f_1 f_2$ for $w_0^1$ and $w_0^2$. Since this product is proportional to differences in weights, a decline in the amount of food available in the environment causes an increase in differences of weights for individuals with greater initial weights, and consequently an increase in the positive skewness of weight distribution.

There is no similarly unequivocal answer if the derivative $\partial y/\partial w_0$ is a decreasing function of the initial weight. Of course, this statemant does not exclude the possibility that the skewness of weight distribution will also increase with deteriorating food conditions in this case.

All the considerations presented above are valid with the assumption that time, in other words the age of organisms, is sufficiently long to consider the limits of functions $f_1$ and $f_2$ instead of (6.21) and (6.22). This means that the approximate equality

$$e^{-a_2(1-b_1)(t-t_0)} \approx 0 \tag{6.26}$$

holds. Referring to the form of the growth curve (6.13), which is the solution of the growth equation used in the model, it should be stated that the satisfaction of the approximate equality (6.26) means that the individual weight approximately equals the final weight $w_\infty$ given by (6.14). Thus, all the described regularities concerning the shape of the weight distribution and its changes in even-aged populations refer to the final stage of individual growth. Since generally the frequency distribution of initial weights is symmetric or negatively skewed then the fact that in the final stage of growth described by the approximate equality (6.26) this distribution becomes positively skewed implies that finally the skewness of weight distribution increases during growth. The appearance of positive skewness in the final stage of growth depends on the relative importance of changes with the initial weight $w_0$ in the term proportional to $\partial y/\partial w_0$ and that proportional to $w_0^{-b_1}$ in the form of function $f_2$ given by (6.22). The relative importance of these two terms of function $f_2$ depends on time. The importance of changes with $w_0$ in the term containing the derivative $\partial y/\partial w_0$ increases with time, as it is proportional to $1-e^{-a_2(1-b)(t-t_0)}$, while the importance of the term with $w_0^{-b_1}$ decreases as it is proportional to $e^{-a_2(1-b_1)(t-t_0)}$. Therefore, a positive skewness for the frequency distribution of weights should be expected earlier, before the final weight is reached and it will continue to increase with time according to the exponentially decreasing effect of the component containing $w_0^{-b_1}$ on the value of function $f_2$. In addition, the positive skewness will appear earlier when food conditions are poor as, according to earlier assumptions, $\partial^2 y/\partial V \partial w_0 < 0$.

### 6.4. *Significance of events at the initial time instant*

Let us construct a model of growth similar to the preceding one but rejecting assumption (3) and relaxing assumptions (1) and (2) (see §6.1). We will leave unchanged only those parts of assumptions (1) and (2) which say that the habitat occupied by an even-aged population is heterogeneous, made up of areas with higher and lower food supply, or that it is homogeneous but divided into areas of unequal size. Thus, we will reject the assumption that the quality of area occupied at the initial time depends on the initial weight. The function $y$ will remain an increasing function of the food supply, $V$, but not of the initial weight

$$y = y(V). \tag{6.27}$$

The growth equation, constructed on the same basis as earlier, will now take the form

$$\mathrm{d}w/\mathrm{d}t = a_1\, y(V)\, w^{b_1} - a_2\, w^{b_2}. \tag{6.28}$$

The solution to this equation for $b_2 = 1$ is

$$w(t) = \left\{\frac{a_1}{a_2} y(V) - \left[\frac{a_1}{a_2} y(V) - w_0^{1-b_1}\right] \mathrm{e}^{-a_2(1-b_1)(t-t_0)}\right\}^{1/(1-b_1)} \tag{6.29}$$

Let us assume that each member of the even-aged population grows according to (6.29). This growth occurs, however, at the different food supplies available for each individual and from different initial weights. Let us consider two individuals with initial body weights $w_0^1$ and $w_0^2$, which grow in areas with food supplies $\epsilon_1 V$ and $\epsilon_2 V$, respectively. After a simple transformation, the difference in weights $w^1(t)$ and $w^2(t)$ of these organisms at time $t$ will be given by

$$\begin{aligned} w^2(t)^{1-b_1} - w^1(t)^{1-b_1} = {} & (a_1/a_2)\,(1-\mathrm{e}^{-a_2(1-b_1)(t-t_0)})\,(y(\epsilon_2 V) - y(\epsilon_1 V)) \\ & + ({w_0^{2}}^{1-b_1} - {w_0^{1}}^{1-b_1})\,\mathrm{e}^{-a_2(1-b_1)(t-t_0)}. \end{aligned} \tag{6.30}$$

Notice that we are considering now differences between $1-b_1$ powers of individual weights. It follows from (6.30) that the difference in the final weights $w_\infty^2$ and $w_\infty^1$ will be described by

$${w_\infty^{2}}^{1-b_1} - {w_\infty^{1}}^{1-b_1} = (a_1/a_2)\,[y(\epsilon_2 V) - y(\epsilon_1 V)]. \tag{6.31}$$

We can get an analogous equation when considering final weights for $b_2 \neq 1$.

Thus, independent of the relation between initial weights at the initial time, after a sufficiently long time the differences in weights will be determined only by differences in the amounts of food available in the areas into which the habitat is divided. The shape of the frequency distribution for weights will be to some extent similar to the frequency distribution of amounts of food $\epsilon_i V, i = 1, \ldots, N$, in the areas where the organisms grow. The differences in the final weights need not be greater than that in initial weights, and it need not depend on the amount of food.

The random distribution of individuals in areas with different food supplies does not permit a description of any pattern in the weight distributions (see §4). Therefore, it is necessary to include assumptions (1) and (2) or (3) in their complete formulation, emphasizing the relation between initial weights and the quality of the areas occupied at the initial time instant.

## 7. A DETERMINISTIC MODEL FOR DIFFERENTIATION OF BODY WEIGHTS: THE CASE WITH A VARIABLE FOOD SUPPLY

We will get a more realistic description than that presented in §6 if we incorporate changes in the concentration or availability of food in the model of individual growth in an even-aged population. Let us consider a system made up of $N$ individuals with initial body weights $w_0^i$, where $i = 1, \ldots, N$. Assume that food supply, if it is not exploited, is increasing at a constant rate $q$, and that it is dispersed in the habitat (or the organisms move in relation to their resources) in such a way that the loss of a portion of food caused by its intake by one individual affects all the other individuals. Let the growth of each of $N$ organisms follow (6.11), and the properties of the model can be analysed without the simplifying assumption that $b_2 = 1$. At such assumptions, changes in $V$, which according to the earlier definition is the average amount of food available for an individual, will be given by

$$\mathrm{d}V/\mathrm{d}t = q - c \sum_{i=1}^{N} a_1\, y(w_0^i, V)\, w^{b_1}, \tag{7.1}$$

where $c$ is a constant coefficient describing the pattern of food distribution in the habitat and assimilation efficiency. For example, if (6.11) is interpreted as at points (1) and (2) in §6.1, this coefficient is determined by the formula $c = (u\,m')^{-1}$, where $m'$ is the number of subareas considered, and $u$ is the coefficient of assimilation efficiency.

According to these assumptions, the growth of all organisms conforms the following system of equations

$$\left.\begin{aligned}
\mathrm{d}w_1/\mathrm{d}t &= a_1\, y(w_0^1, V)\, w_1^{b_1} - a_2\, w_1^{b_2},\\
&\vdots\\
\mathrm{d}w_i/\mathrm{d}t &= a_1\, y(w_0^i, V)\, w_i^{b_1} - a_2\, w_i^{b_2},\\
&\vdots\\
\mathrm{d}w_N/\mathrm{d}t &= a_1\, y(w_0^N, V)\, w_N^{b_1} - a_2\, w_N^{b_2},\\
\mathrm{d}V/\mathrm{d}t &= q - c \sum_{i=1}^{N} a_1\, y(w_0^i, V)\, w_i^{b_1}.
\end{aligned}\right\} \tag{7.2}$$

If the set of equations (7.2) has in the phase space $(w_1, \ldots, w_N, V)$ an equilibrium point $(w_\infty^1, \ldots, w_\infty^N, V_\infty)$, then the coordinates of this point represent the solution to the set of equations generated by equating to zero the right sides of the equations of system (7.2)

$$\left.\begin{aligned}
a_1\, y(w_0^1, V)\, w_1^{b_1} - a_2\, w_1^{b_2} &= 0,\\
&\vdots\\
a_1\, y(w_0^i, V)\, w_i^{b_1} - a_2\, w_i^{b_2} &= 0,\\
&\vdots\\
a_1\, y(w_0^N, V)\, w_N^{b_1} - a_2\, w_N^{b_2} &= 0,\\
q - c \sum_{i=1}^{N} a_1\, y(w_0^i, V)\, w_i^{b_1} &= 0.
\end{aligned}\right\} \tag{7.3}$$

Let us assume that the solution to equations (7.3) exists. Then the set (7.2) is asymptotically stable as there exists for it a Lapunov function, $U$, given by the equation

$$U(w_1, \ldots, w_N, V) = \sum_{i=1}^{N} (w_i - w_\infty^i)^2 + (V - V_\infty)^2. \tag{7.4}$$

Asymptotic stability implies that the individual weights go with time from initial values to some equilibrium weights. Also, the amount of food in the habitat becomes stable at a certain level set by the equilibrium between its input and intake by organisms.

Let us have a closer look at the fates of two individuals with initial body weights $w_0^1$ and $w_0^2$, which are selected from a population of $N$ individuals. Let us assume that the difference in initial body weights is small. Their growth will be described by equations forming a fragment of the set (7.2)

$$\left.\begin{aligned} \mathrm{d}w_1/\mathrm{d}t &= a_1\, y(w_0^1, V)\, w_1^{b_1} - a_2\, w_1^{b_2}, \\ \mathrm{d}w_2/\mathrm{d}t &= a_1\, y(w_0^2, V)\, w_2^{b_1} - a_2\, w_2^{b_2}. \\ &\vdots \end{aligned}\right\} \tag{7.5}$$

Equating the right side of the last equation of the set (7.2), describing changes in the amount of food, to zero, we will get an equation which, in particular, is also satisfied at the equilibrium point $(w_{\infty}^1, w_{\infty}^2, \ldots, V_{\infty})$

$$q = c \sum_{i=1}^{N} a_1\, y(w_0^i, V_{\infty})\, w_{\infty}^{i^{b_1}}. \tag{7.6}$$

If we equate to zero the right sides of the equations describing growth of these organisms, we will get equations that at the equilibrium point take the forms

$$y(w_0^1, V_{\infty}) = (a_2/a_1)\, w_{\infty}^{1^{b_2-b_1}},\quad y(w_0^2, V_{\infty}) = (a_2/a_1)\, w_{\infty}^{2^{b_2-b_1}}. \tag{7.7}$$
$$\vdots$$

Substituting final weights calculated from the equations of the system (7.7) into (7.6), we have

$$q = r_1 \sum_{i=1}^{N} y(w_0^i, V_{\infty})^{r_2}, \tag{7.8}$$

where $r_1 = c a_1 (a_1/a_2)^{b_1/(b_2-b_1)}$, while $r_2 = b_2/(b_2-b_1)$. The parameter $r_2$ is greater than zero, because, as we assumed in (§6.1) $b_2 > b_1$. The parameter $q$, in turn, is the measure of food conditions in the model with variable food concentration or availability. Since $y(w_0^i, V)$ for $i = 1, \ldots, N$ are increasing functions of $V$, it can be concluded from the form of (7.8) that deteriorating food conditions, as related to decreasing $q$, will also result in decreasing $V_{\infty}$ value.

Dividing the equations (7.7) side by side we get

$$\frac{y(w_0^2, V_{\infty})}{y(w_0^1, V_{\infty})} = \left(\frac{w_{\infty}^2}{w_{\infty}^1}\right)^{b_2-b_1}. \tag{7.9}$$

It follows from assumptions made in §6.1 on the properties of function $y(w_0, V)$, the difference between the value of functions $y(w_0^2, V)$and $y(w_0^1, V)$ at fixed $w_0^2$ and $w_0^1$ increases when $V$ is decreasing. Thus, coming back to (7.8) and taking into account what has been said in the preceding paragraph on the relation between $q$ and $V_{\infty}$, it can be stated that for constant values of $w_0^1$ and $w_0^2$ it is possible to find such a small $q$ that

$$\frac{y(w_0^2, V_{\infty})}{y(w_0^1, V_{\infty})} > \left(\frac{w_0^2}{w_0^1}\right)^{b_2-b_1}, \tag{7.10}$$

this being equivalent to

$$\frac{w_{\infty}^2}{w_{\infty}^1} > \frac{w_0^2}{w_0^1}. \tag{7.11}$$

Inequality (7.11) shows that when food conditions are sufficiently poor, the differences in the final weights of growing organisms are larger than the differences in their initial weights. Thus weight differentiation occurs under such conditions. At a sufficiently low $q$, the inequality (7.11) will hold for each pair of individuals in the population of $N$ organisms, and, also for this reason, an increase in the variance of the weight frequency distribution should be expected under these conditions. But when food conditions are sufficiently good, that is, at high values of $q$, the inequality (7.11) will not be satisfied. This implies that the differences in final weights and the variance of the frequency distribution of weights will both decrease.

Let us assume that the derivative $\partial y(w_0, V)/\partial w_0$ is an increasing function of the initial weight, or

$$\partial^2 y(w_0, V)/\partial w_0^2 > 0. \tag{7.12}$$

This assumption means that, as already noted in §6.3, differences in the assimilation of food are greater between individuals with larger initial weights. Thus, the quotient $y(w_0^2, V)/y(w_0^1, V)$ will be larger for pairs of individuals with greater initial weights $w_0^2$ and $w_0^1$, provided these are pairs of individuals with initial weights belonging to different ranges, with only a constant difference in initial weights for each pair. This effect accounts for the development of positive skewness for the frequency distribution of final weights.

These two intensively exploited assumptions on function $y(w_0, V)$ also enable us to prove that deteriorating food conditions account for an increase in the positive skewness of the frequency distribution of final weights. Let us consider two pairs of organisms with initial weights $w_0^2$ and $w_0^1$, and $w_0^4$ and $w_0^3$, such that $w_0^4 > w_0^3 > w_0^2 > w_0^1$ and $w_0^4 - w_0^3 = w_0^2 - w_0^1 = \Delta w_0$, where $\Delta w_0$ is small compared with the weights themselves. Let us consider the situation for two final amounts of food $V_\infty^1$ and $V_\infty^2$ in the environment, given $V_\infty^1 < V_\infty^2$. The positive skewness of frequency distribution of weight will increase with deteriorating food conditions if the quotient of increases in function $y(w_0, V)$ between points $w_0^4$ and $w_0^3$ for the amount of food $V_\infty^2$ and $V_\infty^1$ is greater than that between points $w_0^2$ and $w_0^1$. This quotient, the relation of which to food conditions will interest us, can be expressed by means of the quotient of two derivatives, if $\Delta w_0$ is sufficiently small. Namely, for the pair of initial weights $w_0^2$ and $w_0^1$ we have

$$\frac{y(w_0^2, V_\infty^1) - y(w_0^1, V_\infty^1)}{y(w_0^2, V_\infty^2) - y(w_0^1, V_\infty^2)} \approx \frac{\{\partial y(w_0^1, V_\infty^1)/\partial w_0\}}{\{\partial y(w_0^1, V_\infty^2)/\partial w_0\}}. \tag{7.13}$$

As we assumed earlier, the derivative $\partial y/\partial w_0$ is an increasing function of the initial weight. The assumption that $\partial^2 y/\partial V \partial w_0 < 0$ (see point (7), §6.1) indicates that the numerator of this quotient increases faster than the denominator as the initial weight rises. This means that the quotient (7.13) will be greater for the pair of points $w_0^4$ and $w_0^3$ than for $w_0^2$ and $w_0^1$. Thus, eventually a decrease in the value of $q$, followed by a decrease in the final amount of food in the environment, will bring about a greater, with respect to better food conditions, increase in differences between the values of function $y(w_0, V)$ for pairs of individuals with greater initial weights, which, in turn, implies an increase in the positive skewness of final weights distribution as indicated by the form of (7.9).

The increase in skewness occurs despite the fact that the final weights of at least some individuals are decreasing under deteriorating food conditions. This statement can be inferred from the equation that we obtain on substituting the first $N$ equations of the set (7.3) into (7.6). This yields

$$q = ca_2 \sum_{i=1}^{N} w_\infty^{i b_2}. \tag{7.14}$$

As the frequency distribution of final weights, described earlier, is positively skewed independent of the shape of the frequency distribution of the initial weights (under appropriate food conditions, of course), the latter being most often symmetric, then it follows from this model that the skewness of weight distribution will finally increase with growth of organisms.

The model developed in this section explains the observed properties of weight distributions only on the condition that $\partial^2 y/\partial w_0^2 > 0$. The opposite assumption results in the differentiation of weights under poor food conditions, but the skewness of such a distribution is negative and its absolute value increases under deteriorating food conditions.

Let us note that all the properties of the frequency distribution of weights proved above can be obtained in a slightly changed version of this model. If in the model (7.2) we replaced the assumption that the food increases at constant rate $q$ by the assumption that it increases proportionally to its actual amount if it is not exploited, then $N$ first equations of the set (7.2) remain unchanged, while the last equation will be of the form

$$\mathrm{d}V/\mathrm{d}t = sV - c\sum_{i=1}^{N} a_1\, y(w_0^i, V)\, w_i^{b_1}, \tag{7.15}$$

where $s$ is a constant characterizing the rate of growth of unexploited resources. In this case the equation analogous to (7.8) will be

$$s = r_1 \sum_{i=1}^{N} \frac{y(w_0^i, V_\infty)^{r_2}}{V_\infty}. \tag{7.16}$$

Parameters $r_1$ and $r_2$ have the same values as in (7.8).

In the preceding version of the model, the properties of the frequency distribution of weights were inferred among others from (7.8), which implies that deteriorating food conditions, that is, a decreasing of the value $q$, result in a decrease in the final food resources $V_\infty$. Thus, in this modified form of the model we will also get positively skewed frequency distributions of final weights and all the desired properties of these distributions if, for the appropriate set of equations, there exists a stable equilibrium point and the deteriorating food conditions measured by a decrease in the parameter $s$ cause a decrease in the value of the quotient $y(w_0^i, V_\infty)^{r_2}/V_\infty$ for $i = 1, \ldots, N$, but also in the value of the final amount of food $V_\infty$.

## 8. Stochastic models for differentiation of body weights

### 8.1. *A model with equal probability of taking a food particle*

The deterministic models presented in earlier sections were developed on the assumption that food is available to organisms in a continuous way. Let us consider now the situation in which there is only a certain probability of taking a food particle. For this purpose we will develop a stochastic model of growth and weight differentiation. In the literature there are several versions of stochastic models for growth (for references see Majkowski & Uchmański (1980); in particular Parks (1973)). To analyse the differentiation of weights, it will be most convenient to start with the approach proposed by de Jong (1976) in relation to the growth of larval insects.

Suppose we have an even-aged population of $N$ individuals with equal initial weights $w_0$. Let the food available for members of this population occur in the form of separate particles. The content of food in the environment is described by the variable $V$. It is limited and constant, that is, either continuously replenished, or so large that the removal of a certain number of particles does not change the value of $V$. Let $P(V)$ be the probability of taking a food particle by an organism per unit time. We assume that it is identical for all organisms but it depends on the amount of food in the environment. In one unit of time this individual can take only one food particle, and then its body weight will increase by $g$. Let $P(t, k, V)$ be the probability that by the time instant $t$ inclusive, this individual took $k$ particles of food of the total food supply $V$.

The intake of $k$ food particles in $t$ time units implies that $k$ attempts at catching a particle were successful (the probability of such a single event is $P(V)$), while $t-k$ attempts failed (the probability $Q(V) = 1-P(V)$). Of course $t \geqslant k$. Such events can occur in different order, and their total number equals to $t!/k!(t-k)!$. As a result we get

$$P(t, k, V) = \{t!/k!(t-k)!\} P(V)^k Q(V)^{t-k}. \tag{8.1}$$

The probability distribution of the number of particles taken by time $t$ is identical with the frequency distribution of weights in the same time. As it can be seen from the form of (8.1), the frequency distribution of weights is binomial in this situation. The mean weight $\bar{w}(t)$, variance $\sigma^2(t)$ and skewness coefficient $\gamma(t)$ of the frequency distribution of weights at time $t$ are, respectively,

$$\left.\begin{aligned} \bar{w}(t) &= tP(V), \\ \sigma^2(t) &= t[P(V)-P(V)^2], \\ \gamma(t) &= (1/t)\{[1-2P(V)]/[P(V)-P(V)^2]\}. \end{aligned}\right\} \tag{8.2}$$

The relation of $\sigma^2(t)$ and $\gamma(t)$ to probability $P(V)$ is shown in figure 29. If we assume that $P(V)$ is an increasing function of the amount of food $V$, then for $P(V) < 1/2$ the frequency distributions are positively skewed. The coefficient of skewness declines with increasing $V$, reaching zero (then the distribution is symmetric) for such amounts of food at which $P(V) = 1/2$, and developing a negative skewness when the food supply continues to increase so that $P(V) > 1/2$. When $V$ is constant, skewness tends to zero with time, thus the distribution becomes more and more symmetric.

Summing up, in the situation when food is not taken in a continuous way but there is only some probability of taking a food particle, it is not necessary to assume individual differences in the chance of taking a particle to obtain skewed weight distributions; it is enough to assume that the probability $P(V)$ is equal and independent of the number of food particles taken at earlier time instances. However, the weight distributions obtained in this way can be only binomial distributions.

### 8.2. *A model with unequal probabilities of taking a food particle*

Let us consider a situation similar to that described in §8.1, but assuming that the probability of taking a food particle in a unit of time depends on the number of particles taken earlier, that is, on the weight of the organism and on the food supply available in the environment. Let

$$P_i(V) = P(w_0+ig, V) \tag{8.3}$$

be the probability of taking a food particle, when the amount of food available is $V$, by an individual which has already taken $i$ food particles, that is, its body weight is $w_i = w_0+ig$, where $w_0$ is the initial weight, and $g$ is the increase in weight after taking a food particle. Let $Q_i(V)$

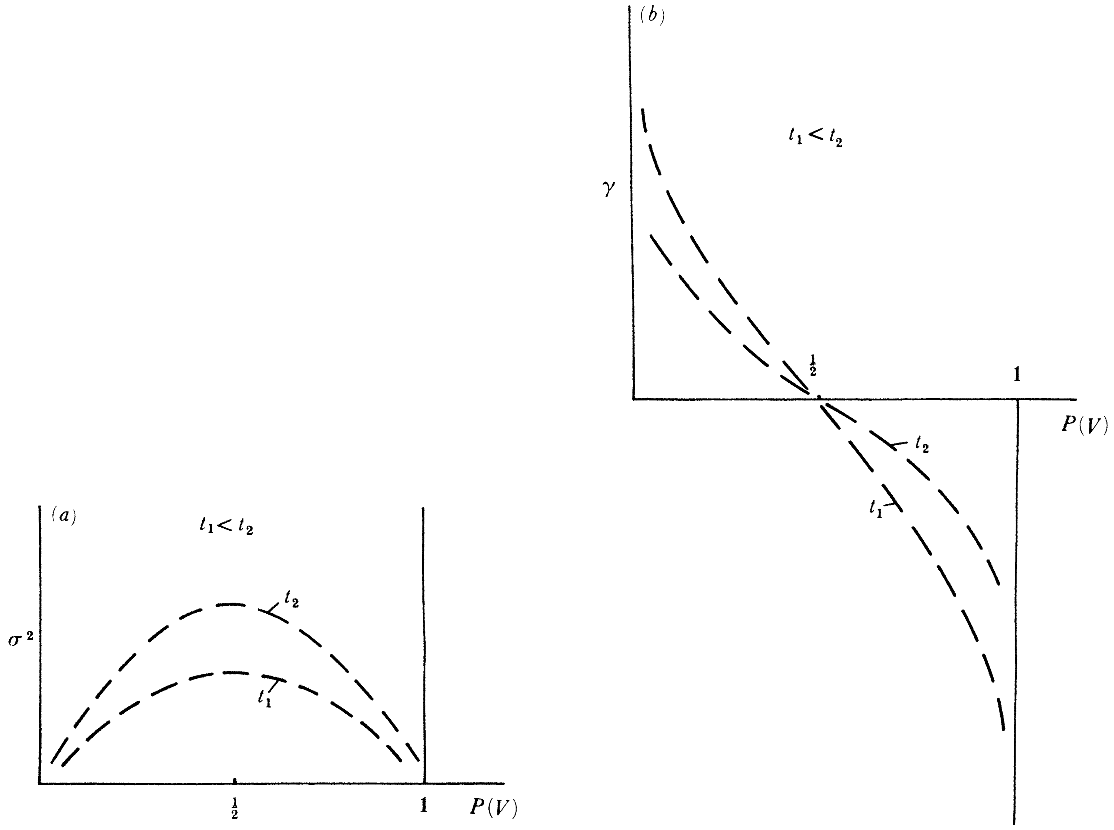

FIGURE 29. Stochastic model with equal probability $P(V)$ of taking a food particle: (a) relation between variance $\sigma^2$ of weight distribution and probability $P(V)$; (b) relation between skewness $\gamma$ and $P(V)$. Dependences on time are shown.

be the probability of failure in taking a food particle by the individual with weight $w_i$ at the amount of food $V$. Then

$$Q_i(V) = 1 - P_i(V). \tag{8.4}$$

We assume that function $P(w, V)$ satisfies the following conditions (figure 30).

(1) It is an increasing function of weight at a constant, thought not optimal, food supply. This means that for $w_1 < w_2$ and $V$ is constant, we have

$$P(w_1, V) < P(w_2, V). \tag{8.5}$$

(2) For an individual with a constant body weight it is an increasing function of food supply in the environment, that is, for $V_1 < V_2$ and $w$ is constant, we get

$$P(w, V_1) < P(w, V_2). \tag{8.6}$$

(3) In the absence of food, the probability of taking a food particle is equal to zero, independent of weight

$$P(w, 0) = 0. \tag{8.7}$$

(4) Under optimum food conditions, when it is assumed that food supply is unlimited ($V = \infty$), the probability of taking a food particle does not depend on weight too and it is equal to a certain constant $a$, where $a \leqslant 1$

$$P(w, \infty) = a. \tag{8.8}$$

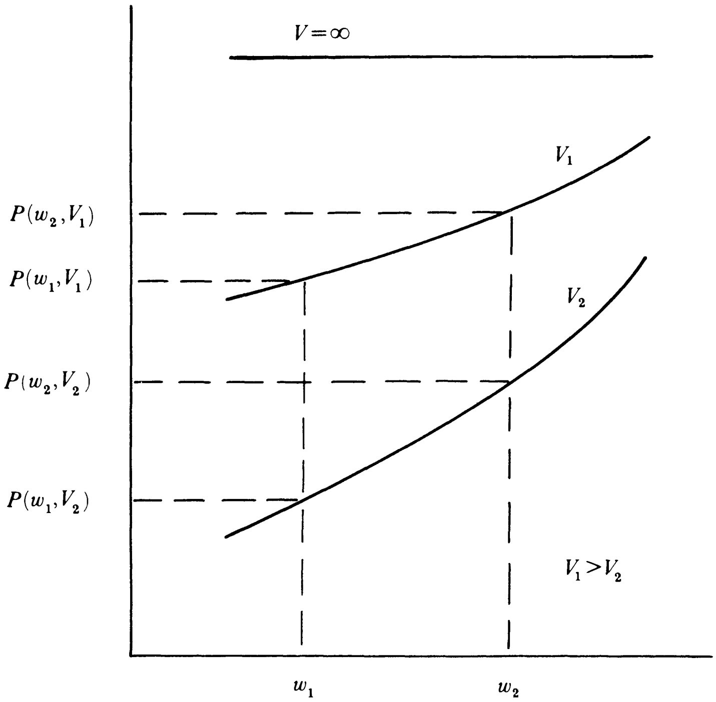

FIGURE 30. Theoretical shape of function $P(w, V)$ describing probability of taking a food particle in a stochastic model of weight differentiation. Assumptions concerning dependence on resource availability or concentration and body weight are illustrated.

(5) The differences in the probability of taking a food particle for individuals with different weights increase with the deterioration of food conditions. This means that for $V_1 < V_2$ and $w_1 < w_2$ we have

$$P(w_2, V_2)-P(w_1, V_2) < P(w_2, V_1)-P(w_1, V_1). \tag{8.9}$$

(6) Deterioration of food conditions causes a greater decrease in the probability of taking a food particle for lighter than for heavier individuals, or for $V_1 < V_2$ and $w_1 < w_2$ there is

$$P(w_1, V_2)-P(w_1, V_1) > P(w_2, V_2)-P(w_2, V_1). \tag{8.10}$$

Let $P(t, k, V)$ be the probability that the individual will take $k$ food particles in $t$ units of time at the amount of food $V$, that is, its body weight at time $t$ will be $w_k = w_0+kg$. This individual is successful in taking food particles in $k$ units of time and unsuccessful in $t-k$ units of time (assuming that $t \geqslant k$). To calculate the probability $P(t, k, V)$ the sum should be calculated for the probability of all events including $k$ successes and $t-k$ failures. Differences among these terms lie in different way in which $k$ successes and $t-k$ failures can be arranged on $t$ positions. The formula describing $P(t, k, V)$ will be made up of two terms. The one is equal to $\Pi_{i=0}^{k-1} P_i(V)$ independent of the sequence of successes and failures, and the other one describes all the possible arrangements of failures. Each of the $t-k$ positions can be filled with only one value of probability $Q_i(V)$, where $i = 0, \dots, k$. Finally, the probability $P(t, k, V)$ is given by the equation (developed by Miłosz Michalski)

$$P(t, k, V) = \prod_{i=0}^{k-1} P_i(V) \sum_{i_h=0}^{k} Q_{i_h}(V) \sum_{i_{h-1}=i_h}^{k} Q_{i_{h-1}}(V) \dots \sum_{i_1=i_2}^{k} Q_{i_1}(V) \tag{8.11}$$

where $h = t-k$. The shape of the distribution given by (8.11) is identical to the weight distribution at time $t$. It is difficult, however, to analyse its properties in this form. Instead, we can analyse two functions that estimate function $P(t, k, V)$ from above and below. Notice that two inequalities are satisfied:

$$\frac{t!}{k!\,(t-k)!}\,Q_k(V)^{t-k}\prod_{i=0}^{k-1}P_i(V) < P(t,k,V) \tag{8.12}$$

and

$$P(t,k,V) < \frac{t!}{k!\,(t-k)!}\,Q_0(V)^{t-k}\prod_{i=0}^{k-1}P_i(V). \tag{8.13}$$

Equations (8.11), (8.12) and (8.13) will still be valid if for $k = 0$ we assume that $\prod_{i=1}^{k-1} P_i(V) = 1$.

Let us find the values of estimating functions in relation to $k$ at constant $t$ and $V$ (figure 31). As it follows from the Pascal triangle (Hellwig 1968), the number of combination $t!/k!\,(t-k)!$ for fixed $t$ is symmetrically increasing and decreasing about the middle point of section $(0, t)$. $Q_0(V)^{t-k}$ is an increasing function of $k$ because $Q_0(V) < 1$. Similarly, $Q_k(V)^{t-k}$ is increasing from $Q_0(V)^t$ at $k = 0$ to 1 at $k = t$. But for each value of $k$, not equal to 0 or $t$, we have

$$Q_k(V)^{t-k} < Q_0(V)^{t-k} \tag{8.14}$$

because the probability of taking a food particle is greater for an individual which has already taken $k$ particles than for individual which have taken zero particles, and $P_i(V)$ and $Q_i(V)$ are related as in (8.4).

The value of the term $\prod_{i=0}^{k-1} P_i(V)$ decreases with increasing $k$, because $P_i(V) < 1$ for each $i$. According to the earlier assumption, this term reaches the highest value equal to 1 for $k = 0$.

The terms $Q_k(V)^{t-k}\prod_{i=0}^{k-1} P_i(V)$ and $Q_0(V)^{t-k}\prod_{i=0}^{k-1} P_i(V)$ take the value $Q_0(V)^t$ at $k = 0$, they reach maxima when $k$ increases, and then they tend to $\prod_{i=0}^{t-1} P_i(V)$ at $k = t$. $Q_i(V) < Q_0(V)$ for $i \neq 0$ as it follows from assumption (1) in §8.2 and from (8.4). Thus, under poor food conditions

$$\prod_{i=0}^{t-1} P_i(V) < Q_0(V)^t. \tag{8.15}$$

At the same time, the first term given at the beginning of this paragraph is less than the second one for each $k$ not equal to 0 or $t$.

Thus each of the functions limiting the probability $P(t, k, V)$ (see inequalities (8.12) and (8.13)) is a product of two functions: the values of the first one are symmetric about the middle of the section $(0, t)$, while the second one reaches its maximum within this section. Note that this maximum shifts towards lower values of $k$ when the probability $P_i(V)$ takes smaller values, that is, under poorer food conditions. We may expect, therefore, that when food conditions are sufficiently poor, the shape of the two limiting functions will be similar to positively skewed distributions, and the frequency distribution of weights $P(t, k, V)$ contained between them will probably have a skewness coefficient greater than zero.

Let us also note that the previously mentioned shifting of the maxima of functions limiting the distribution $P(t, k, V)$ towards lower values of $k$ with decreasing $V$, implies an increase in the skewness of weight distribution caused by a decline in the available food supply.

With the course of time, however, the maxima of limiting functions shift towards increasing values of $k$ because functions $Q_k(V)^{t-k}$ and $Q_0(V)^{t-k}$ decrease with increasing $t$. Thus, it may be expected that at a constant food supply available in the environment the skewness coefficient

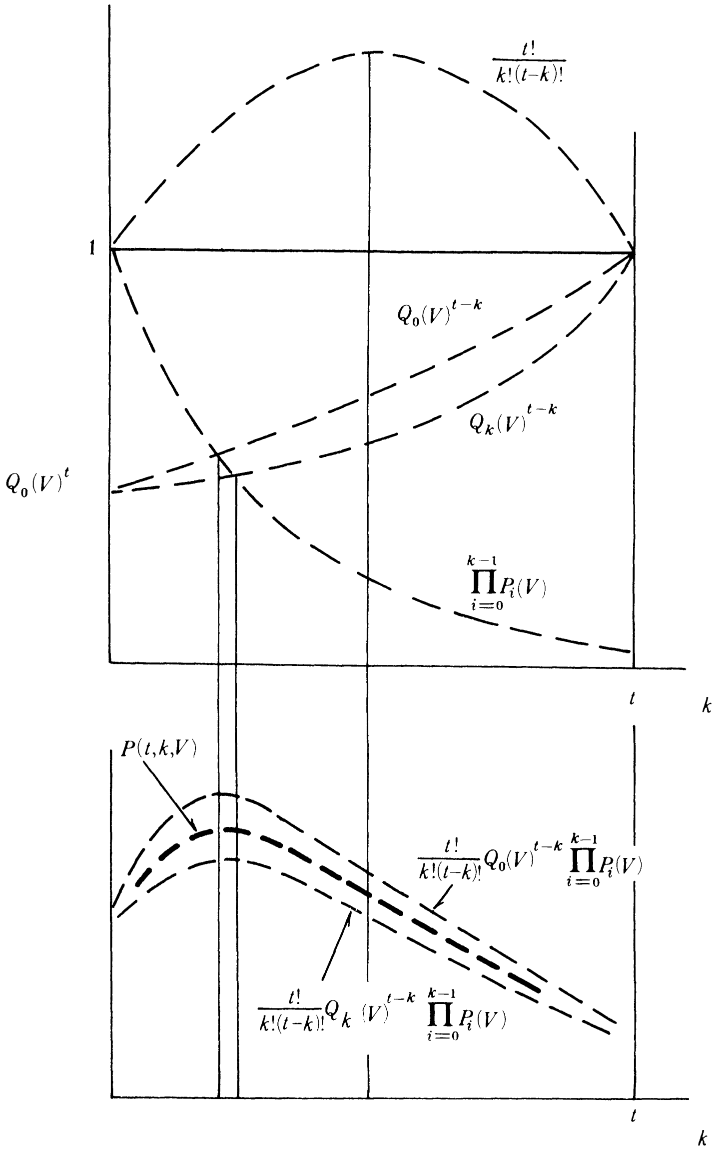

Figure 31. Factors included in the functions limiting probability $P(t, k, V)$ and their relation to the number $k$ particles of food taken. (For details see text.)

of weight distribution in the even-aged population of individuals, the growth of which is described by a stochastic model, will decline with time.

The methods applied above to prove the properties of the distribution $P(t, k, V)$ is an approximate method, because conclusions are based on the behaviour of the functions setting upper and lower limits on the distribution of weights. In fact, the analysis of this kind only reinforces our conviction that the distribution $P(t, k, V)$ has the desirable properties, but it cannot totally exclude the existence of quite opposite properties of this distribution.

A more detailed study was presented by Kimmel (1984), who achieved deep analytical results, though at the expense of the generality of the model. After presentation of the stochastic model with the probability of taking a food particle depending only on the weight of individual (that is, in the constant food conditions), and proving that in this situation, being positive at the beginning, skewness quickly decreases with time to the negative values, the author considered the situation, which to some extent is the stochastic version of the model with variable food conditions. First the model of 'hard' competition is presented, in which only one food particle is consumed in each discrete time step. Later, this assumption is relaxed and in the second version of the model, with the 'mild' form of competition, more than one individual can consume a food particle at each time step. These processes were ended when all food particles given at the beginning were used. The probability of the taking of one particle of food by an individual was in both versions direct proportional to its weight and inversely proportional to the number of food particles consumed in the population by this time. The author has obtained positively skewed weight distributions and indicated that in these models strong dependence between skewness of weight distribution and number of competing individuals exists.

The models presented by Kimmel (1984) are, however, distorted by one assumption. It is intuitively clear that the competition would be stronger in poorer food conditions and we expected that it would be reflected in the changes of shape of weight distribution. On the other hand, in the above models there is very specific dependence on food conditions. They describe the results of food exhaustion, but, owing to assumptions concerning the probability of an individual taking a food particle (it is inverse proportional to the number of particles already consumed by all individuals), it is impossible to compare these processes under various food conditions. The number of food particles present in the environment at the beginning estimates only the duration of this process, but its actual number did not influence directly the probability of taking a food particle.

### 8.3. *Stochastic models involving energy losses and changes in food supply*

In the stochastic models of growth developed in preceding sections respiratory losses were neglected or (and it does not make difference in terms of mathematical description) it was assumed that the respiration per time unit is a constant, independent of the weight fraction of the food particle taken by an organism, while it equals zero in time units when the organism failed to take a food particle.

A more realistic model should incorporate energy losses for living activity, for example, for foraging, etc. We can make a simplifying assumption that the respiration in a unit of time is not related to the success or failure in taking food in this time, but it depends on the actual weight of an individual. This relationship can be presented in the form of the power function given by (6.10). Thus, preserving the general pattern and symbols from the preceding models, we assume that the individual with the weight $w(t)$ at time $t$ will have the weight

$$w(t+1) = w(t)+g-\alpha w(t)^{\beta} \tag{8.16}$$

with probability $P(w(t), V)$ and the weight

$$w(t+1) = w(t)-\alpha w(t)^{\beta} \tag{8.17}$$

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

In this case it is difficult to give an analytical form of the probability $P(t, k, V)$, and to examine its properties. For this reason it was decided to simulate these stochastic processes with a computer. This approach additionally makes it possible to simulate growth under a variable food supply in the environment. The analysis of changes in food supply in preceding versions of the stochastic model, examined by an analytical method, was beyond the author's scope.

The growth $N$ individuals was followed. The value of $N$ was selected to be sufficiently large to get a reliable frequency distribution of weights. At the initial time instant all the individuals had equal body weights $w_0$. After each time step a number was drawn for each individual from the uniform distribution on section $(0, 1)$ and it was compared with the probability $P(w, V)$ corresponding to this individual. If it was lower, the weight was increased by $g$, if it was greater than the probability the weight did not increase. In both cases, respiration was subtracted according to (8.16) or (8.17). The simulation was run at constant food supply over the whole process, or only in particular units of time. In the latter case, the food supply in each successive time step was diminished by the total consumption of all individuals in the population in the preceding time step.

Various forms of the function $P(w, V)$ were fitted, including that proposed by Łomnicki (1980*b*)

$$P(w, V) = 1-\mathrm{e}^{-c'wV}, \tag{8.18}$$

where $c'$ is constant, and also the relationship

$$P(w, V) = (wV)/(d+wV), \tag{8.19}$$

where $d$ is another constant. At $w = 0$ we get $P(0, V) = 0$ for both these functions. Thus for small values of $w$, they do not satisfy assumptions (5) and (6) from §8.2, but for an appropriately chosen range of weights both these functions satisfy all the assumptions required. Notice that functions (8.18) and (8.19) are concave, that is, $\partial^2 P/\partial w^2 < 0$.

Also an equation was applied which enabled us, through changes in parameters, to generate a whole family of relationships

$$P(w, V) = a\ \mathrm{e}^{-c'V}\left(\frac{w}{d}\right)^l + a[1-(1+p)\ \mathrm{e}^{-c'V}], \tag{8.20}$$

where $a$, $d$, $c'$, $p$ and $l$ are positive constants. When $l = 1$ and $V$ is a constant this equation is a linear function of $w$. An increase in the value of $V$ is followed by a decrease in the slope of these lines, while the intersection point with the vertical axis moves upwards. When $l \neq 1$, function (8.20) behaves in a similar way, the only difference being that for $l > 1$ this is a convex function ($\partial^2 P/\partial w^2 > 0$), while for $l < 1$ concave ($\partial^2 P/\partial w^2 < 0$) at fixed $V$. For small values of $V$, function $P(w, V)\,|_{V=\text{constant}}$ given by (8.20) intersects the $w$-axis. Then it was assumed that $P(w, V) = 0$ for weights smaller than the weight corresponding to the intersection point and above this point (8.20) was applied. It was also assumed that there is a maximum weight setting the upper limit on the weights of individuals in the population. In all these assumptions it is always possible to choose such parameters in (8.20) that if $V = 0$, we will get $P(w, 0) = 0$ for each $w$. Function (8.20) satisfies, with one exception, all the assumptions made in §8.2. When $P(w, V)\,|_{V=\text{constant}}$ intersects the $w$-axis, the mathematical form of assumptions (5) and (6) is not satisfied for small $w$. However, this is not incompatible with the biological reality behind these assumptions since further deterioration of food conditions cannot affect the individuals that already have zero chance of taking a food particle.

As a result of all simulations, we obtained positively skewed weight distributions and the skewness increased with time. It also increased when in simulations with constant food supply the value of $V$ was decreased, or when the initial food supply was decreased and food was continuously exploited (figure 32). It is worth noticing that the increase in skewness of distribution under deteriorating food conditions has often led to the situation in which maximum weight was higher at poor than at good food conditions, though the mean weight decreased. The skewness of weight distribution decreased only in extreme cases, when food shortage was so heavy that almost all individuals had a zero probability of taking a food particle. Thus they lost weight all the time, their weights being very small and almost uniform.

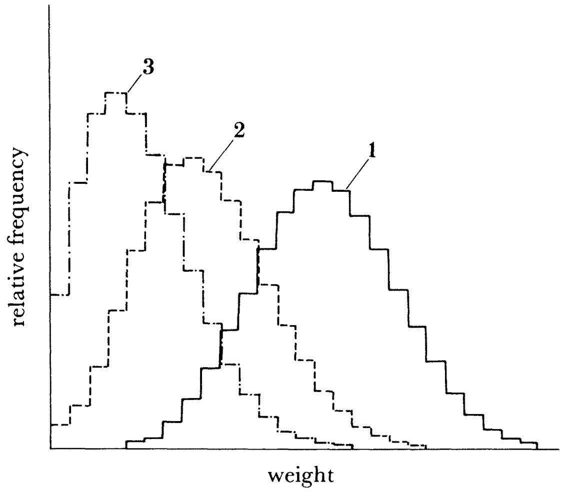

FIGURE 32. An example of simulation of growth and differentiation of weights by using function (8.20) in different food conditions (various $V$). Almost symmetric weight distribution was obtained in the best food conditions (1); skewness increases with deterioration of food conditions (distributions 2 and 3, respectively).

The application of different forms of function $P(w, V)$ describing the probability of taking a food particle, that is, the partitioning of resources among members of the population, is reflected in the shape of the distribution, in the value of skewness coefficient and in the time of appearance of positively skewed distributions. By using function (8.20) with different values of the parameter $l$, it has been observed that skewness may be much more easily obtained (with respect to the time of appearance of positively skewed distributions) in the case of convex functions, that is, such functions that $\partial^2 P/\partial w^2 > 0$. This is consistent with properties of the deterministic models for weight differentiation, where for convex functions only describing the partitioning of resources among individuals it was possible to prove the development of positive skewness in weight distributions.

The second essential property of function $P(w, V)$ seems to be whether or not it passes through the origin of the coordinate system, that is, whether for $w \to 0$ also $P(w, V) \to 0$ at fixed $V$. If so, then after a sufficiently long time or under sufficiently poor food conditions, the frequency distribution of weights develops a second maximum in the neighbourhood of zero, in addition to the main maximum. It is formed by very small, 'slowly dying' individuals. In view of the shape of function $P(w, V)$ they have little chance of taking a food particle and their respiration is also small because of their small weights. As a result, these individuals lose weight very slowly. There is no such effect and weight distributions are unimodal, when probability $P(w, V)$ tends to a value greater than zero for weights tending to zero.

The above situations result from the unrealistic assumption that the individual weight can decline to zero. Assuming that there is a threshold weight and that individuals with weights less than this threshold are eliminated, we would get unimodal weight distributions with all the desired properties. It follows from these considerations that if we take the ratio of the number of individuals below the threshold weight to the total number of individuals as a measure of mortality, then it would appear that the mortality is higher for the population in which resources are partitioned according to function $P(w, V)$ with a property

$$\lim_{w \to 0} P(w, V)\,|_{V=\text{constant}} = 0. \tag{8.21}$$

This implies that resource partitioning has an effect on population dynamics.

## 9. Summing-up and discussion

### 9.1. *Skewness in frequency distributions of body weights*

The models presented in §6–8 explain the existence of positive skewness for weight distribution in even-aged populations, as well as causes of changes in this skewness, which are presented in §4. The deterministic models describe and explain the following points:

(1) the occurrence of positively skewed weight distributions in even-aged populations;

(2) the increase in skewness of weight distributions with time at a constant density and a constant food supply in the environment;

(3) the increase in skewness at increasing density and declining food supply in the environment. The effect of food supply on the shape of the weight distribution has been analysed in preceding sections, but the effect of density needs explanation. Note that the food supply $V$ in deterministic models is, as mentioned earlier, an average amount of food available for one individual. On the other hand, in all the quoted experiments and observations the increase in density means the increase in the number of individuals in a space of a fixed size. Obviously, this must be followed by a decrease in the average amount of food per individual. Thus, the increase in density in these models has an effect on the shape of weight distributions through a decline in the amount of food available for particular individuals. Such results can be obtained in models with a constant food supply over the period of growth as well as in the models in which unexploited food increases exponentially or at a constant rate.

The stochastic models describe and explain the same properties:

(4) the occurrence of positive skewness for weight distributions in even-aged populations;

(5) the increase in skewness when the food supply declines or when the density increases. In stochastic models, it is not assumed that $V$ is an average amount of food available for one individual. It is possible, however, to assume this, and then, as in deterministic models, the increase in density will act through a decrease in the amount of food available per individual. However, if there is no such assumption, it still may be expected that an increase in density at fixed $V$ will lower the probability of taking a food particle and, as a result, the skewness of weight distribution will increase. Such results were obtained in the stochastic model with constant food supply by using an analytical approach and, in models with variable food supply, by using computer simulation of growth with the original food supply being continuously exploited.

(6) In stochastic models, however, the skewness of weight distribution decreased with time for populations with constant densities and constant food supplies.

Two aspects of weight differentiation seem to be most important: the shape of the frequency distribution of weights and the pattern of changes in this shape. It has been proved in this study that competition and uneven partitioning of resources give rise to the development of positive skewness for weight distribution. The readiness of generation of a positive skewness in weight distribution for even-aged populations, when all the types of models presented here for wide class of functions of food partitioning among individuals are used, is in agreement with the common occurrence of this phenomenon in Nature. However, changes in the shape of the distribution involve two groups of problems: the effect of changes in the population density and food supply on the shape of the distribution, and its changes with time. In all the models skewness increased when the food supply in the environment declined or when the population density increased. The original mechanism explaining these two relationships is, as the presented models show, deteriorating food conditions. Much less clear is the problem of the relationship between the skewness of weight distribution and time for even-aged populations of growing individuals. An increase in skewness with time, as was the case in the experiments described earlier, was obtained in the deterministic model with a constant food supply, but in the stochastic model at the same food conditions this effect was difficult to observe. This inclines us to suggest that there is no general pattern in changes of the skewness of weight distribution with time. The only general conclusion is that the weight distribution has positive skewness in even-aged populations and this skewness increases under deteriorating food conditions. Changes in skewness with time, however, should be viewed as a result of specific ecological situations. The author tends to consider food conditions during the observation under natural or experimental conditions as a factor responsible for changes in skewness with time.

An increase in skewness with time observed by Koyama & Kira (1956) (see §2) in experiments with plants and also occurring in natural plant and animal populations can be explained by the deterministic model with a constant density and constant food supply. It can also be explained by stochastic and deterministic models with variable food supplies, provided the resources are not replenished but become exhausted as a result of exploitation. The original increase in skewness with time and its decrease after reaching a peak, this pattern being observed by Mohler *et al.* (1978, see §2) for natural plant populations, can be explained, according to the suggestions of the authors, as above, until the peak is reached and then by a decrease in the number of individuals in the population. Thus, it can also be explained by a decrease in density as a result of natural thinning, which occurred during the period of maximum skewness in weight distribution.

### 9.2. *Differentiation of body weights*

Problems concerned with weight differentiation are closely related to the shape of weight distribution. In deterministic models skewness appeared when the differences in individual weights increased and this increase was uneven: to get a positive skewness it is necessary that the differences between larger organisms be greater than between smaller organisms.

The deterministic models presented in this study suggest the following conclusions.

(1) In the model with a constant food supply in the environment there is a certain threshold of food supply below which differences in weights among individual organisms grow with time, while above this threshold weights become uniform. The population density in this model has a similar effect on weight differentiation: a decrease in the amount of food available per individual at high densities accounts for an increase in differences between weights.

(2) In deterministic models with variable food supply deterioration of food conditions or an increase in density also give rise to an increase in differences in weights among individuals.

The conclusions concerning differences in weights are also valid for the variance of the weight distribution, since the latter is proportional to the average square of weight differences in the population. It can be stated, therefore, that in situations described by deterministic models the variance of weight distributions will increase with deteriorating food conditions or with increasing population densities.

For stochastic models we may state the following.

(3) At equal probabilities of taking a food particle the variance of the weight distribution decreases with declining probability of capturing a food particle for such values of the latter for which a positively skewed weight distribution is produced. This variance also increases with time.

(4) In stochastic models with unequal food partitioning a decrease in food supply or an increase in density gave rise in some cases to an increase in the variance of the distribution, as indicated by computer simulations (no analytical solutions were found).

Few experimental data on the differentiation or the variance of weight distribution discussed in §§2 and 3 do not provide the basis for sufficiently unequivocal conclusions to compare them with detailed outputs of the models. But general conclusions seem to support what was stated in §4, and it may be concluded that, at least in the case of unequal food partitioning the improvement of food conditions or a decrease in population density give rise to the equalization of weights (differences in weights or the variance of the distribution of weights are reduced), while the deterioration of food conditions or an increase in population density account for differentiation of weights.

### 9.3. *Is competition responsible for differentiation of weights and skewness of their distributions?*

It is not easy to decide whether the skewness of weight distribution and the differentiation of weights are the results of interactions among individual organisms or only of the growth process itself. I do not know papers based on experiments designed to answer this question. As far as I know (this paper was written during 1980–1982) nobody has made attempts at observing the weight distribution in even-aged populations with no interactions among their members.

In the explanations presented so far it has been stated that the positive skewness of weight distribution is a natural consequence of the exponential character of growth (see the paper by Koyama & Kira discussed in §4). Intraspecific competition was considered as a factor of secondary importance, which could only reinforce the effects of growth itself. The conclusions made by Koyama & Kira can be put in question in two ways.

(1) The use of the exponential equation to describe growth is of limited value as this equation can describe at most initial phases of growth.

(2) No attempt was made at constructing a model involving the effect of competition on skewness and differentiation of weights. A suggestion that competition can affect growth through changes in the distribution of the parameters of the model built by Koyama & Kira (1956) (see §4) do not propose any mechanisms that could have a reasonable biological interpretation.

To sum up, the Koyama & Kira (1956) models do not explain the underlying mechanism generating changes in the skewness of weight distribution related to changes in food conditions and population density. They only indicate that in some situations these distributions can develop a positive skewness.

Other models constructed to explain the development of skewness in weight distributions are of similar value. This is also the case of Koch's papers (1966, 1969) (see §4), in which it is proved that the distribution of each variable obtained as a product of linear dimensions is identical or similar to the log-normal distribution. Unfortunately, the general character of the statements, lack of biological interpretation and ignorance of experimental results account for the fact that these models cannot be used as a tool for interpretation of skewness and its changes under variable food conditions and population densities.

The author's intention was to show that only competitive interactions among members of even-aged populations underlie the observed patterns. But do the models presented here really describe competitive interactions? Two individuals compete with each other when one of them gains something also needed by the other and it is in limited supply. For this reason competitive interactions are, as it seems, involved in the forms and in particular in the properties of functions $y(w_0, V)$ and $P(w, V)$. In addition, the models with variable food supply (deterministic and stochastic) describe competition for food because they refer to a situation in which all individuals use the common resource pool that is constantly diminished by the quantities taken by particular organisms. It seems, however, that the deterministic and stochastic models with constant food supply can describe, in addition to the real competition, independent growth of isolated individuals. Thus, it can be seen that it is possible to obtain a positively skewed distribution of weights through an appropriate choice of food conditions in an experiment with isolated individuals. The shape of this distribution will be identical to that involving competitive interactions, provided we perform such manipulation of food conditions for each individual so that the assimilation by particular individuals will be the same in both cases. I expect, however, that in both situations, there will be differences in assimilation under identical food conditions and, therefore, we will obtain identical weight distributions only under different food conditions.

To answer the question that is in the title of this section, we need to consider two problems.

(3) Are the properties of weight distributions in even-aged populations, described above, a result of competitive interactions?

(4) Must these interactions also be reflected in the uneven resource partitioning among members of the even-aged population so that we could explain all properties of weight distributions as dependent on them?

The models presented in this study prove that the answer to both these questions should be positive. Competitive interactions among members of even-aged populations enables us to build models of growth and differentiation which adequately describe and explain all the observations: the occurrence of positive skewness and the differentiation of weights under deteriorating food conditions or at increasing population density. To obtain all these effects concerning changes in the skewness of weight distributions, we have to assume, at least in the case of deterministic models, that competitive interactions have as one of their effects an uneven partitioning of resources among individuals in the population. In stochastic models this assumption also leads towards skewed weight distributions with the desired properties, but skewed distributions can also be obtained when the resources are evenly partitioned.

In the situation when there are no interactions among individuals, the frequency distribution of weights should be a result of intrinsic variability in growth processes, which is put into the model as a random variability in the parameters of the equations. At the beginning of growth, when it can be considered as exponential, provided the growth rate per unit of individual weight in the population has a normal distribution, this effect is well described by the Koyma & Kira (1956) model. According to their esults, a log-normal weight distribution may be expected. In later periods of growth, when the growth curve approaches the saturation level, the frequency distribution of weights should be of the shape that we can get when taking into account the variability of the parameters of the Bertalanffy, Winberg or the balance equations incorporated in the formulas for final weights (see Appendix 2: comments to equations (B 8) and (B 15)). Assuming that these parameters have normal distributions in the population (this seems to be a reasonable assumption when there are no interactions among individuals), we should also expect that the final weights will be positively skewed.

Two factors are responsible for the differentiation of weights in even-aged populations: one is competitive interactions among individuals. These interactions can explain the relation of the differentiation and skewness of weight distribution to population density and trophic conditions. The other factor is the genetic variability in growth of particular individuals. The decrease in weight differentiation under favourable food conditions, as described in §6.2, is apparently due to the relaxation of competitive interactions. Under improving food conditions or at decreasing population density the variance of the distribution of weights will approach the variance of the distribution resulting from genetic variability in weight.

Therefore the statement that competitive interactions imply skewed weight distribution is misleading since it suggests a mutual unequivocal relation between these two concepts, whereas the reciprocal statement need not be true. It would be more important to say that competitive interactions among members of even-aged populations are responsible for an increase in the positive skewness of weight distributions when food conditions are getting poor or when the population density is increasing, or both.

The differences between frequency distributions of weights generated by interactions among individuals and those resulting from intrinsic variability in growth probably lie in the shapes of these distributions, if any differences exists. It follows from the papers by Koyama & Kira (1956) that in the exponential phase of growth the frequency distribution of weights is log-normal without competitive interactions. This is supported by Koch in papers cited earlier. In the stochastic model of growth with the equal partitioning of resources a binomial weight distribution was obtained. This way of looking for differences, however, may be illusory because of difficulty in determining the shape of weight distributions that should correspond to different ecological situations, and also owing to the weakness of statistical methods used to recognize frequency distributions.

### 9.4. *Organisms described by the models*

The general classification of the models presented in this study into deterministic and stochastic corresponds to the classification into plants and animals. Animals, whether carnivores or herbivores, in a more or less heterogeneous environment have, in many cases, only a certain chance of finding food. In this situation the stochastic model is most appropriate. Plants, however, which are competing for light and nutrients (Donald 1963), can take food in an approximately continuous way. Thus, deterministic models can describe well growth and differentiation of land plants, planktonic organisms, including plants and animals, as well as all other animals feeding by filtration.

The models discussed in this study have one feature in common: they describe the situation where each individual interacts with all the other individuals by using the same resource pool. This fact leads to the conclusion that the models of differentiation for plants describe competition for nutrients rather than for light. The model of competition for light must consider the spatial structure, that is, the distribution of individuals in space, shape of the canopy and the height structure. An intense competition for light in one place need not mean that light is deficient in another place. Therefore, it is not true that each individual interacts with all the other individuals. Of course, this classification should take into account many exceptions: the spatial distribution of individuals may also influence the competition between plants for nutrients, as well as competition between animals, especially in a heterogeneous environment. However, spatial aspects of weight differentiation were not considered in the present models: they need a separate analysis. The first attempt was made by Gates (1978, 1982). Recently Wyszomirski (1983) studied, in parallel to the work presented here, the shape of weight distribution and its changes when spatial distribution of individuals should be taken into account.

### 9.5. *Restrictions of the models*

The stochastic and deterministic models of weight differentiation developed in this study describe only the situations predicted by the assumptions presented in §§6–8. They hold when food is in excess or when population density is low, also at a moderate food shortage or population density. They cannot be used, however, for high densities or severe food shortages, as the above assumptions will not be satisfied. It should be expected that under extremely poor conditions functions $y(w_0, V)$ and $P(w, V)$ will equal zero over the whole range of weight variability or they will take a constant value close to zero, which implies that food conditions are so poor that weight has no effect on food intake. It is also possible that in these situations only some individuals take food. Then the functions $y(w_0, V)$ or $P(w, V)$ will equal zero for small weights, while they will take values greater than zero starting from a certain weight. To make the description more realistic under such extreme conditions, the elimination of individuals should be introduced into the model.

Therefore, we cannot expect that all conclusions listed in §§9.1 and 9.2 will hold under severe food deficiency or high population density. Under these extreme conditions weight distributions, their skewness and variance, can behave in different ways.

### 9.6. *Verifications of the models*

Two conclusions not directly arising from the assumptions and not supported experimentally so far, have been obtained as a result of the analysis of the models.

(1) In the deterministic model with constant food supply there is a certain threshold value of food below which differentiation of weights occurs during growth, and above which weights become uniform.

(2) To obtain desirable changes in positive skewness of weight distribution with changes in food supply and population density in deterministic models, it is necessary to assume that the function $y(w_0, V)$ for $V$ equal to a constant, is a convex function of $w_0$, that is, $\partial^2 y/\partial w_0^2 > 0$. In the case of stochastic models, as the computer simulation has shown, the assumption that the function $P(w, V)$ is convex for $V$ equal to a constant, much facilitated the development of positive skewness of weight distributions.

Both these conclusions should be experimentally verified. Their possible rejection would put in question the validity of the models for weight differentiation presented in this study. The first conclusion can relatively easily be verified in experiments, while the biological interpretation and the verification of the second conclusion is much more difficult. The assumption that $y(w_0, V)$ or $P(w, V)$ are convex functions of $w$ or $w_0$ means that the difference in the amount of assimilated food between two individuals of similar weights will increase with rising weights. Therefore, the answer to the question of whether both these functions are convex can be reduced, in fact, to decide how much an individual could gain if it had the rank of his close neighbour in weight hierarchy. In the case of the convex functions $y(w_0, V)$ and $P(w, V)$ a heavier individual will gain more. Let us imagine a situation already described in §6, where a new generation colonizes an area subdivided into patches, say, with different food supplies. If in this situation more severe competition, as measured by the frequency and intensity of conflicts, is observed between heavy than between light individuals, this may be an indication that the partitioning of resources is described by a convex function.

### 9.7. *Differences between the deterministic and stochastic models*

The two types of the models differ in the 'easiness' with which they generate the differentiation of weights and skewed weight distributions. In stochastic models positive skewness can be obtained when the resources are evenly partitioned among individuals and the initial weights of all organisms are identical. Uneven resource partitioning and differences in initial weights exaggerate skewness. To obtain skewness in deterministic models it is necessary to make an assumption that resources are unevenly partitioned and initial weights are differentiated.

The initial differences in weights may be caused by many factors. They may be due to the lack of synchronization in life cycles of particular individuals in even-aged populations. Black & Wilkinson (1963) and Ross & Harper (1972) have found a correlation between the time of sprouting and the subsequent weight of plants. Greater weights were reached by plants sprouting earlier, the differences in weights being higher than expected only on the basis of differences in timing of growth. Similar effects are also produced in animals. Bryant (1978) observed the hierarchy of weights in nesting house martins *Delichon urbica*. Hatching was asynchronous. The earliest nestlings were already feeding while the last eggs were incubated. This accounted for differences in weights, which were maintained over the growth period.

Another cause of differences in weights in the early stages of growth can be the heterogeneity of the habitat on a scale that differentiates growth conditions for individual organisms. Such mechanisms of weight differentiation for plants were suggested by Stern (1965), Obeid *et al.* (1967) and Harper (1977). We can imagine similar mechanisms working in sessile animals or in territorial animals if the environment is not homogeneous.

The models considered in this study give a somewhat deeper insight into the mechanisms underlying the development of skewness in weight distributions. As it has been found for deterministic models, which are generally used to describe growth in plants, all the considerations on the effect of the initial differentiation (thus also environmental heterogeneity) require a supplemental assumption that at the initial time instant the heavier individual occupies a better position, gaining an advantage in this way, and it is being maintained throughout the period of growth.

All this suggests that the value of skewness coefficient, its changes, as well as differences in weights among individuals, largely depend on the biology of growth, this being reflected in different models of growth, but they also depend on environmental effects on growth. This is one more argument against Koyama & Kira's views.

### 9.8. *Functions used in the models*

One of the bases used to construct models presented in this paper is the assumption that resources are unevenly partitioned among members of even-aged populations. It is introduced into the deterministic model by the function $y(w_0, V)$ and into the stochastic models by the function $P(w, V)$ relating the food intake or the probability of food intake to the food supply in the habitat and the initial weight (in the deterministic model) or the actual weight (in the stochastic model).

The functions of partitioning of resources among individuals in the population (in this study functions $y(w_0, V)$ or $(Pw, V))$ are, in my opinion, the most proper description of intraspecific competition. This study presents, on the basis of analysis of weight distributions in even-aged populations, some of their general properties. However, I do not know of published work that would provide more detailed information on these functions. There are no models predicting their properties in particular ecological situations. We can imagine that the effect of food will be such as found in studies on the effect of the concentration and availability of food on consumption and weight increases, and it can be described, for instance, by the Ivlev (see §6.1) or Michaelis–Menten function. However, the effect of weight or initial weight can only indirectly be found, for instance, through the analysis of the distributions of births or sprouting of particular seeds over time, or from their distribution in a heterogeneous environment.

There is some indirect information on the derivative $\partial y/\partial w_0$. Bryant (1978) has noted that the hatching period of successive nestling house martins is more prolonged if food conditions are poor during egg laying. As we already know, this gives rise to a greater differentiation of initial weights, therefore it can be expected that the derivative $\partial y/\partial w_0$ will also increase, provided the growth of nestlings can be described by the deterministic model. Ford (1975) found a relation between the relative growth rate and the individual weight at different stages of the development of the plant population. In the first period, when the population density is high, the relative growth rate linearly increases with plant weight, the slope of this line being very high. In later periods of population development, when the population density declines owing to natural thinning, the relation between the relative growth rate and weight ceases to be linear and the differences in growth rates decrease. Although the relative rate of growth (net increase per unit weight) is not equal or proportional to $y(w_0, V)$ or $P(w, V)$ (gross increase), Ford's findings can be an indication that improving food conditions can lead to a decrease in the value of derivative $\partial y/\partial w_0$ or $\partial P/\partial w$.

### 9.9. *Differentiation of body weights and population dynamics: application of the models for differentiation of body weights*

The classical model describing dynamics of a single population (May 1973, 1976; May & Oster 1976) in its differential form is

$$\mathrm{d}N/\mathrm{d}t = f(N) \tag{9.1}$$

and the difference form of this equation is

$$N_{t+1} = f(N_t), \tag{9.2}$$

where $N$, $N_t$ and $N_{t+1}$ denote numbers or densities of individuals, while $t$ and $t+1$ are time instants. Most often the form of the function $f$ is such that the increase in density is greatest for small densities and declines with increasing densities.

This pattern includes the Malthus model of exponential growth with $f(N) = rN$ in differential form, the Verhulst logistic equation, for which $f(N) = rN\,[1-(N/K)]$, the Gompertz model with $f(N) = rN \ln(K/N)$, and also many other models applying different forms of the function $f(N)$.

The basis of all models for population dynamics is the description of mechanisms underlying mortality, migrations and reproduction. Traditional, density-dependent models, based on concepts developed by Verhulst, Volterra and Lotka hardly explain these mechanisms at all. For instance, the relation between population density and mortality, even described by a certain function, is only an expression of statistical correlation between these variables: the real mechanism is hidden somewhere deeper. The basis of the classical models for number dynamics of a single population is an assumption that everything that is going on in the population and that has an effect on its dynamics depends only on the density of the population. In particular, the resources available for particular members of the population are not considered and single organisms are treated as uniform, unchangeable molecules, without life cycles, growth or differences between individuals. This approach has often been criticized (recently, for example, by Łomnicki 1980*b*; Kozłowski 1980).

There are very few papers proposing anything other than classical solutions to this problem. Fuji (1975) has constructed a simulation model of number dynamics for a cohort of insects, in which developmental stages are taken into account. The model describes interactions among individuals in different developmental stages. They involve predator–prey interactions between adult and larval individuals, on the one hand, and all the other stages, as well as interactions among adults resulting in a reduction in the number of eggs laid. The mathematical description of these interactions is of the Volterra model type; thier intensity depends on the number of encounters between individuals of interacting developmental stages, which leads to a typical density-dependent relationship. The model involves individual growth. The initial egg weight and the parameters of growth equations for particular developmental stages are considered as individual-specific properties. The rate of growth in active periods depends on food supply in the environment. It is assumed that at the initial time instant there was a certain amount of food available, which was gradually used up with time. Transition to the next developmental stage depends on the attainment of an appropriate critical weight, and if the weight declined below this threshold value, the individual was eliminated. Qualitative conclusions from this model are consistent with the results of laboratory experiments on insect populations.

Another approach to population dynamics with non-overlapping generations was proposed by Matessi (1980). This model involves the dynamics of resources used by the population, which are replenished at a constant rate, subject to self-destruction in proportion to their amount, and which are harvested in proportion to the number of consumers. The model also considers growth of individuals in the population in relation to the amount of resources, but it is assumed that all individuals grow in an identical way. The life span of one generation is determined by the time of growth from the initial weight to a certain stationary value. When growth is completed, new individuals of the next generation are produced. The objective of this model is to describe changes in numbers over the life span of one generation, as well as changes in the number of young and adult individuals in successive generations. For this purpose it is assumed that growth follows a certain standard curve. The number of individuals at a given time instant decreases when the actual weight at this instant is less than the standard weight, the number of individuals eliminated per unit of time being proportional to the difference between these two weights. The number of young produced at the end of the generation time is, in turn, proportional to the excess of weight of adult individuals compared with the standard weight. In this model, rich in mathematical analysis, the author developed an analytical formula relating number of young individuals in successive generations.

Differences between individuals and the effect of these differences on the dynamics and stability of populations with non-overlapping generations are considered in the models proposed by Łomnicki (1978, 1980*a*, *b*). All members of the population are ranked. The amount of food taken by an individual over its life span depends on its rank and on the food supply in the environment. If food intake is greater or equal to a certain fixed value, the individual produces offspring in a number related to the amount of food above this fixed value. If it is less than this threshold value, the individual dies without producing offspring. This model, which from a mathematical point of view is a set of difference equations, describes changes from generation to generation in the size of the population and in the exploited resources. It is also possible to redefine the assumptions of this model to get a similar description of the population with overlapping generations, by using a set of differential equations (Uchmański 1983).

There is no space here to estimate the biological relevance of these models. We may only state that they are the result of a compromise between the mathematical simplicity and an exact copy of Nature. The latter tendency, as the response to the biological primitivism of classical models, is a common denominator of all new approaches to population dynamics. It will probably not be possible to reconcile this tendency with attempts at developing a single general model. The future rather belongs to detailed models of selected populations.

Of course, various models which are, to some degree, general can stress different points in considerations concerning population dynamics. The model proposed by Łomnicki did it with respect to the individual differences between members of population (he also discussed all consequences of this phenomenon). Let us go one step further and, remembering what was said in the Introduction to this study, stress once more that the description of the intraspecific competition (together with the individual differences) is the most proper way of discussing the population dynamics of the single population. To do so, we should relate in some way the amount of resources taken by a particular individual with its future fate. The models of weight differentiation presented in this study may be useful in these efforts. They enable us to describe population dynamics with respect to individual life cycles, individual growth, dynamics of exploited resources, differences among individuals and, of course, intraspecific competition. This approach stems from the papers by Łomnicki quoted earlier.

Let us assume that in the *j*th generation of a population with non-overlapping generations there are $N_j$ individuals with initial weights $w_0^i$, where $i = 1, \ldots, N_j$, at the initial time instant. They feed on food that is replenished at a constant rate and, at the same time, continuously exploited. The increase in weights depends on the initial weights and on the food supply in the habitat. Then the growth of individuals of the *j*th generations, if it is deterministic, can be described by the set of equations analogous to (7.2)

$$\left.\begin{aligned} \mathrm{d}w_1/\mathrm{d}t &= a_1\, y(w_0^1, V)\, w_1^{b_1} - a_2\, w_1^{b_2}, \\ &\vdots \\ \mathrm{d}w_{N_j}/\mathrm{d}t &= a_1\, y(w_0^{N_j}, V)\, w_{N_j}^{b_1} - a_2\, w_{N_j}^{b_2}, \\ \mathrm{d}V/\mathrm{d}t &= q - c \sum_{i=1}^{N_j} a_1\, y(w_0^i, V)\, w_i^{b_1}. \end{aligned}\right\} \qquad (9.3)$$

Let an individual be eliminated from the cohort when its weight drops below a certain minimum value $\tilde{w}$, i.e. if

$$w_i(t) < \tilde{w}. \tag{9.4}$$

In particular the elimination through comparison with the threshold value can take place at the end of the growth period, when $t \to \infty$. Let us also assume that after the completion of growth only the individuals with final body weights $w^i_\infty$ greater than another threshold weight $\hat{w}$ can reproduce. The number $\eta_i$ of offspring produced by a particular individual is, as proved many times, a power function of the adult weight

$$\eta_i = \alpha' w^{i\beta'}_\infty \tag{9.5}$$

or it is proportional to the difference between $w^i_\infty$ and $\hat{w}$

$$\eta_i = \delta(w^i_\infty - \hat{w}), \tag{9.6}$$

where $\alpha'$, $\beta'$ and $\delta$ are constants. Finally, assume that the initial weights of the progeny of the $i$th individual have a normal distribution about the initial weight of the parent organism. The progeny of all the individuals that attained the reproductive state represent the next generation, the changes in numbers of which can be described by the present model (figure 33).

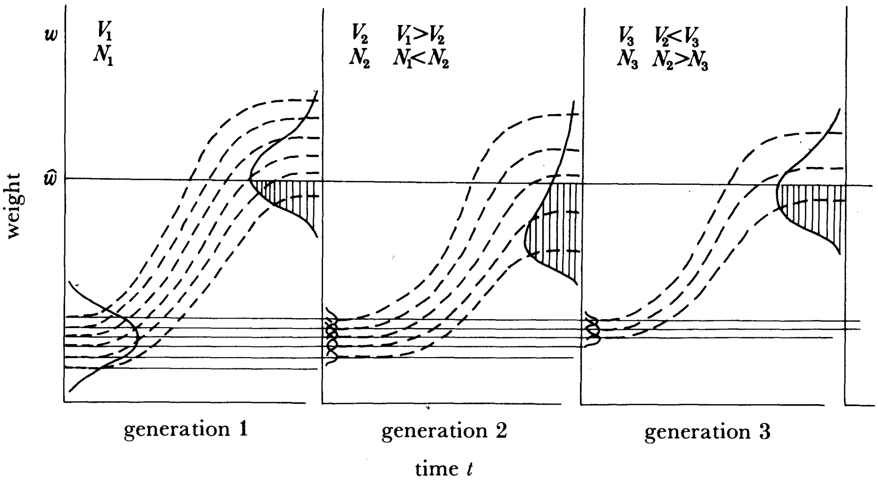

FIGURE 33. An illustration of the population model constructed on the basis of the model of weight differentiation. Changes of weight distribution over three generations are shown together with food conditions and number of individuals in each generation. The example illustrates the situation when the system started from good food conditions ($V_1$ relatively high) and a small number of individuals $N_1$. Successive changes in $V$ and $N$ are shown.

Note that this model describes number dynamics of parthenogenetic individuals or females in the case when offspring are similar to mothers. But a simple modification, in the simplest case the introduction of a constant sex ratio and some rule of heredity for weight, will make it possible to describe the dynamics of the whole sexual population.

The above model can also work with another mechanism of the elimination of individuals from the cohort. For example, let the individual be removed when it can take very little or no food at all for a certain number of time units. This model can also contain a different description of individual growth since the stochastic model of growth, described in §8, also fits it.

It is not true, as has been assumed by classical population models, that the mortality due to other reasons than predation acts instantaneously and constantly. It is rather a long process of differentiation ended by the death of weaker individuals. For an illustrative example let us look at the sets of individual growth curves of the nestling tree swallow *Iridoprocne biocolor* presented by Zach & Mayoh (1982) (figure 34) and house wrens *Troglodytes aedon* presented by Zach (1982). This is from the population dynamics point of view, which is assumed in the model proposed in this section.

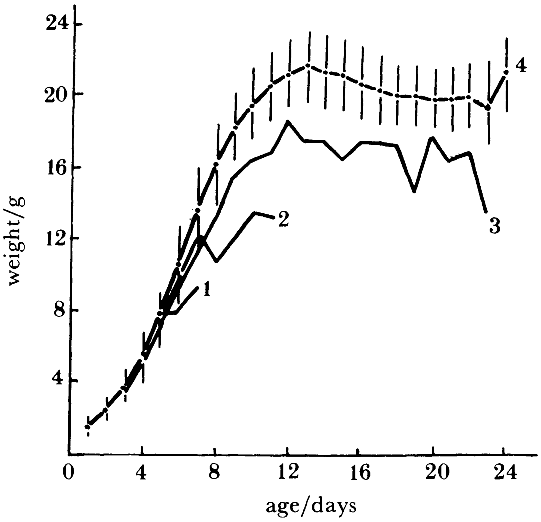

Figure 34. Growth curves of the nestling tree swallow *Iridoprocne bicolor*: 4, the average growth curve for fledged tree swallows, vertical bars indicate ±1 s.d. about average values; 1, 2, 3, growth curves for individuals that died earlier for the reasons other than predation. (Redrawn from Zach & Mayoh (1982).)

Let us note that in this model the regulation of number of individuals should be expected. If the number of individuals in the population is high in a certain generation, then the resources will be heavily exploited and, consequently, individual weights will be reduced. Thus the mortality rate will increase and the production of offspring will decrease. As a result, the number of individuals in the next generation will be reduced. The same line of reasoning shows that when the abundance of a certain generation is low, it will increase in the next generation.

The scheme presented here of the construction of the model of population dynamics ensures a great elasticity of description. It involves different ways of getting food (deterministic and stochastic models of growth), different ways of partitioning resources among population members (forms of functions $y(w_0, V)$ and $P(w, V)$) and also different causes of elimination from the population. Owing to changes in the form or parameters of the equation describing the food supply in the habitat, it is also possible to analyse population dynamics in different types of environments, such as constant environments and with variable food supply, of permanent and of limited duration. It also enables us to describe the population dynamics of species with different bioenergetics, with different proportions of assimilation, respiration and reproduction in the energy balance. Ecological bioenergetics accumulated a large body of information on consumption, respiration, weight increase and its relation to food conditions, etc. This is a rich source of parameters and relationships for the models of this type, and has so far hardly been used at all. Population models of this type make it possible to combine bioenergetics with the theory of population dynamics, so far developed independently.

The description of population dynamics on the basis of models for the differentiation of individuals creates the possibility of a deeper investigation into the mechanisms of number regulation. An outline of such a model presented in this section enables us to follow relationships between natality and mortality, on the one hand, and various forms and intensities of competition, concentration and availability of food and life cycles of organisms, on the other. A simple computer simulation carried out in this study for the stochastic model of weight differentiation shows that there is a clear relationship between mortality and the way of partitioning resources within the population.

In addition to the theoretical analysis of population dynamics and number regulation, practical advantages of the models developed here can be of great importance. They can prove to be useful in the optimization of population management, where the standing crop with a particular size structure is an important variable. For example, in a model for fishing we may consider the problem of producing individuals of equal weights, or of maximizing the number of individuals in selected size classes, or to optimize food supply, to maintain a desired size structure in the population.

Adam Łomnicki was the first to have noticed almost all problems considered in this study. I express my gratitude to him for the inspiration and for making the problems interesting for me. The encouragement of Professor Romuald Z. Klekowski was of major importance during preparation of the manuscript. I thank all who discussed the early drafts of this study with me. Especially helpful were the comments of Tomasz Wyszomirski, but I also express my thanks to Marek Kimmel and many others. Adam Godzik assisted me during preparation of §8.3. I am grateful to Barbara Diehl for translation into the English language.

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## Appendix 1. Distributions of weights

Let $N$ be the number of individuals in a group. We denote by $w_i$ the weight of the $i$th individual, where $i = 1, \ldots, N$. It is possible to establish some weight classes and numbers of individuals with weights falling within particular classes. This can be presented in the form of a histogram which is called the distribution of weights in this group of organisms. It is characterized by the mean weight, $\bar{w}$, in this group

$$\bar{w} = \frac{1}{N} \sum_{i=1}^{N} w_i \tag{A 1}$$

and by the variance, $\sigma^2$, which is the measure of the breadth of the distribution

$$\sigma^2 = \frac{1}{N} \sum_{i=1}^{N} (w_i - \bar{w})^2. \tag{A 2}$$

Given the mean and the variance, the distribution can assume different shapes. The weight most frequently represented in the group is called the mode. If the mean weight is equal to the mode, the distribution is symmetric. The distributions that do not show this property are called skewed distributions. If the mode is greater than the mean weight, the distribution is skewed to the left. If the opposite is true, the distribution is skewed to the right. The measure of the shape of the distribution is the coefficient $\gamma$, also called the coefficient of skewness of the frequency distribution

$$\gamma = \frac{\frac{1}{N}\sum_{i=1}^{N}(w_i-\bar{w})^3}{\left[\frac{1}{N}\sum_{i=1}^{N}(w_i-\bar{w})^2\right]^{\frac{3}{2}}}. \tag{A 3}$$

The coefficient of skewness is zero for symmetric distributions, less than zero for the distributions skewed to the left and greater than zero for those skewed to the right. Its absolute value is the measure of the degree of skewness (figure 35).

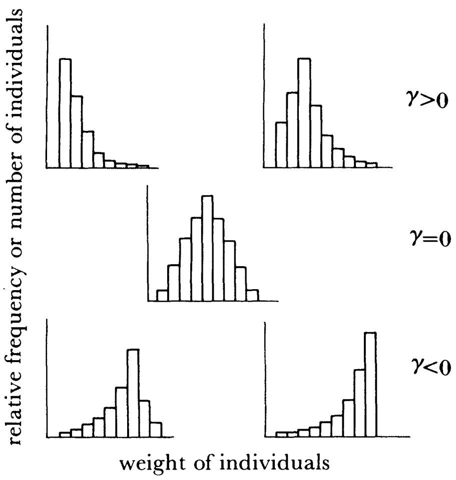

FIGURE 35. Various shapes of weight distributions. Upper line: positively skewed distributions; (upper left histogram, L-shaped distribution); middle line: symmetric distribution, bottom line: negatively skewed distributions, (bottom right histogram, J-shaped distribution).

If the width of weight classes used to draw a histogram are gradually reduced, then at the width tending to zero the distribution of weights can be described by a continuous function $g(w)$, called the density of weight distribution. The number of individuals with weights in the interval $w$ and $w+\Delta w$, where $\Delta w$ is small relative to $w$, is equal to $Ng(w)\,\Delta w$.

## APPENDIX 2. CHOSEN DETERMINISTIC GROWTH EQUATIONS

In this appendix the commonly used deterministic growth equations will be presented. A full description of these and other deterministic growth equations is to be found in Majkowski & Uchmański (1980).

(1) Equation of exponential growth. This description of the growth assumes that in each time unit the increase in weight is equal to some constant part of the actual weight, that is

$$\mathrm{d}w/\mathrm{d}t = r'w, \tag{B 1}$$

where $r'$ is a constant. The solution to this equation is of the form

$$w(t) = w_0\,\mathrm{e}^{r'(t-t_0)}, \tag{B 2}$$

where $w_0$ is the initial weight at initial time instant $t_0$. Equation (B 2) describes the unlimited growth of the weight.

(2) The Bertalanffy equation. One of the first growth equations was constructed by Pütter. His equation was further developed by Bertalanffy and is traditionally called the Bertalanffy equation. This equation is of the form

$$\mathrm{d}w/\mathrm{d}t = F_1(w,t) - F_2(w,t), \tag{B 3}$$

where $F_1(w,t)$ is the rate of anabolism or the rate of synthesis of building materials depending on the weight and time (age of the organism) and $F_2(w,t)$ describes the rate of catabolism or the rate of degeneration of building materials. Pütter assumed that the rate of anabolism is directly proportional to the rate of consumption and the rate of consumption is directly proportional to the intestine surface. He also assumed isometric growth and in this way he found that the rate of anabolism was proportional to the 2/3 power of the body weight, while the rate of catabolism was proportional to the body weight. Thus he got the formula

$$\mathrm{d}w/\mathrm{d}t = Hw^{\frac{2}{3}} - Kw, \tag{B 4}$$

where $H$ and $K$ are constants.

Inconsistency between experimental growth curves and the curves constructed on the basis of (B 4) contributed to the modification of this equation and to the formulation of its new interpretation. Bertalanffy proposed the use of the resting metabolism as a measure of the rate of anabolism because the resting metabolism most closely corresponds to that when the growth process only is responsible for energetic losses. There is a power relationship between the respiratory rate and the body weight of an individual, with the exponent varying between 2/3 and 1. Thus the anabolic term in the Bertalanffy equation was of the form

$$F_1(w,t) = Hw^m, \tag{B 5}$$

where $H$ is constant and $2/3 \leqslant m \leqslant 1$. The catabolic term was assumed to be of the form

$$F_2(w,t) = Kw. \tag{B 6}$$

It leads to the following equation of growth, named the Bertalanffy equation

$$\mathrm{d}w/\mathrm{d}t = Hw^m - Kw. \tag{B 7}$$

The solution to this equation (and to (B 4) for $m = 2/3$) is of the form

$$w(t) = w_\infty\left(1-\left(1-\left(\frac{w_0}{w_\infty}\right)^{1-m}\right)\mathrm{e}^{-(1-m)K(t-t_0)}\right)^{1/(1-m)} \tag{B 8}$$

where $w_\infty = (H/K)^{1/(1-m)}$ and $w_0$ is the initial weight at initial time instant $t_0$. The growth curve described by (B 8) is limited and S-shaped, $w_\infty$ is final weight to which $w$ tends when $t \to \infty$.

The Winberg equation also has the same shape as (B 7), but its interpretation and the way the parameters are estimated is different from the Bertalanffy equation.

(3) Balance equation. The law of conservation of energy and matter relates the instantaneous production of the organism $P$ to the rates of instantaneous assimilation $A$ and respiration $R$

$$P = A - R. \tag{B 9}$$

When all production is only an increase in weight (there is no reproduction, etc.)

$$P = \mathrm{d}w/\mathrm{d}t \tag{B 10}$$

substituting (B 10) to (B 9) gives us the so-called balance equation of growth

$$\mathrm{d}w/\mathrm{d}t = A - R. \tag{B 11}$$

If we assumed, according to numerous experimental data, that the consumption $C$ and respiration rates are power functions of body weight, that is

$$C = a_1' w^{b_1} \tag{B 12}$$

and

$$R = a_2 w^{b_2}, \tag{B 13}$$

then, on condition that $u$, the coefficient of efficiency of food assimilation, is constant, we get

$$\mathrm{d}w/\mathrm{d}t = a_1 w^{b_1} - a_2 w^{b_2} \tag{B 14}$$

where $a_1 = a_1' u$. This equation, like the Bertalanffy equation, describes limited growth according to an **S**-shaped growth curve. The final weight $w_\infty$ is given by

$$w_\infty = (a_1/a_2)^{1/(b_2-b_1)}. \tag{B 15}$$

## APPENDIX 3. DIFFERENTIATION AND FREQUENCY DISTRIBUTIONS OF BODY WEIGHT IN CHOSEN DETERMINISTIC GROWTH EQUATIONS

(1) Exponential equation of growth. Let us consider an even-aged population consisting of $N$ organisms. Assume that $g(w_0)$ is the density of the frequency distribution of weights at the initial time $t_0$ and $g(w)$ is the density of the frequency distribution of weights at time $t > t_0$. These distributions are related as follows

$$g(w_0)\,\mathrm{d}w_0 = g(w)\,\mathrm{d}w. \tag{C 1}$$

The mean initial weight $\bar{w}_0$ is given by

$$\bar{w}_0 = \int_0^\infty w_0\, g(w_0)\,\mathrm{d}w_0 \tag{C 2}$$

while the mean weight $\bar{w}$ at time $t$ is

$$\bar{w} = \int_0^\infty w g(w)\,\mathrm{d}w. \tag{C 3}$$

According to (B 2) (see Appendix 2) and (C 1), we will get the following relation between the mean weights at time $t$ and $t_0$

$$\bar{w} = \mathrm{e}^{r'(t-t_0)} \int_0^\infty w_0\, g(w_0)\,\mathrm{d}w_0 = \mathrm{e}^{r'(t-t_0)}\,\bar{w}_0. \tag{C 4}$$

Thus, the mean weight increases exponentially.

The variance $\sigma_0^2$ of the distribution of initial weights is given by

$$\sigma_0^2 = \int_0^\infty (w_0 - \bar{w}_0)^2\, g(w_0)\,\mathrm{d}w_0 \tag{C 5}$$

while the variance $\sigma^2$ at time $t > t_0$ equals to

$$\sigma^2 = \int_0^\infty (w-\bar{w})^2 g(w)\,\mathrm{d}w. \tag{C 6}$$

By using (B 2), (C 1) and (C 4), we can present (C 6) in the form

$$\sigma^2 = \int_0^\infty [w_0\,\mathrm{e}^{r'(t-t_0)} - \bar{w}_0\,\mathrm{e}^{r'(t-t_0)}]^2 g(w_0)\,\mathrm{d}w_0 = \mathrm{e}^{2r'(t-t_0)}\,\sigma_0^2. \tag{C 7}$$

Therefore, during exponential growth the variance also increases exponentially.

The variability coefficient $\delta$ of the weight distribution at time $t > t_0$ is given by

$$\delta = \frac{\surd\sigma^2}{\bar{w}} = \frac{\surd(\mathrm{e}^{2r'(t-t_0)}\,\sigma_0^2)}{\bar{w}\,\mathrm{e}^{r'(t-t_0)}} = \frac{\surd\sigma_0^2}{\bar{w}_0} = \delta_0, \tag{C 8}$$

where $\delta_0$ is the variability coefficient of the frequency distribution of initial weights. It follows from this that the variability coefficient remains constant during exponential growth, though the variance of the distribution increases.

The third moments of the weight distributions $\mu_3^0$ and $\mu_3$ at time $t_0$ and $t$ respectively are given by

$$\mu_3^0 = \int_0^\infty (w_0-\bar{w}_0)^3 g(w_0)\,\mathrm{d}w_0 \tag{C 9}$$

and

$$\mu_3 = \int_0^\infty (w-\bar{w})^3 g(w)\,\mathrm{d}w. \tag{C 10}$$

By using a similar transformation we will get

$$\mu_3 = \int_0^\infty [w_0\,\mathrm{e}^{r'(t-t_0)} - \bar{w}_0\,\mathrm{e}^{r'(t-t_0)}]^3 g(w_0)\,\mathrm{d}w_0 = \mathrm{e}^{3r'(t-t_0)}\,\mu_3^0. \tag{C 11}$$

Thus the third moment increases exponentially. The coefficient of skewness $\gamma$ is described by the equation

$$\gamma = \frac{\mu_3}{(\sigma^2)^{\frac{3}{2}}} = \frac{\mathrm{e}^{3r'(t-t_0)}\,\mu_3^0}{(\mathrm{e}^{2r'(t-t_0)}\,\sigma_0^2)^{\frac{3}{2}}} = \frac{\mu_3^0}{(\sigma_0^2)^{\frac{3}{2}}} = \gamma_0, \tag{C 12}$$

where $\gamma_0$ is the coefficient of skewness for the distribution of initial weights. This implies that the exponential growth does not change the skewness of weight distribution.

(2) The Bertalanffy and Winberg equations. Let us assume that two individuals have similar weights $w_0$ and $w_0+\Delta w_0$ and $\Delta w_0$ is small. We may examine time-related changes in the difference in weight $\Delta w(t)$ between these individuals. They will be described by the general equation

$$\Delta w(t) = \frac{\partial w(t)}{\partial w_0}\Delta w_0. \tag{C 13}$$

From (B 8) we obtain for the Bertalanffy equation

$$\frac{\partial w(t)}{\partial w_0} = \left(\frac{H}{K} - \left(\frac{H}{K} - w_0^{1-m}\right)\mathrm{e}^{-K(1-m)(t-t_0)}\right)^{m/1-m} \mathrm{e}^{-K(1-m)(t-t_0)}\,w_0^{-m}. \tag{C 14}$$

Substituting (C 14) into (C 13) we get the description of changes in differences of weights with time when growth follows the Bertalanffy equation

$$\Delta w(t) = \left(\frac{H}{K} - \left(\frac{H}{K} - w_0^{1-m}\right) \mathrm{e}^{-K(1-m)(t-t_0)}\right)^{m/(1-m)} \mathrm{e}^{-K(1-m)(t-t_0)}\, w_0^{-m}\, \Delta w_0. \tag{C 15}$$

To facilitate the analysis of the behaviour of (C 15), we may use the following

$$f_1' = \left(\frac{H}{K} - \left(\frac{H}{K} - w_0^{1-m}\right) \mathrm{e}^{-K(1-m)(t-t_0)}\right)^{m/(1-m)} \tag{C 16}$$

and

$$f_2' = \mathrm{e}^{-K(1-m)(t-t_0)}\, w_0^{-m}. \tag{C 17}$$

The difference $\Delta w(t)$ in individual weights will increase when the product $f_1' f_2'$ is greater than one and it will decrease when it is less than one. The function $f_1'$ is a strictly increasing function of time and

$$\lim_{t\to\infty} f_1' = \left(\frac{H}{K}\right)^{m/(1-m)} \tag{C 18}$$

while $f_2'$ is a strictly decreasing function of time and

$$\lim_{t\to\infty} f_2' = 0. \tag{C 19}$$

For $t = t_0$ we have from (C 16) and (C 17)

$$f_1'(t_0) f_2'(t_0) = 1. \tag{C 20}$$

It follows from (C 18) and (C 19) that the product $f_1' f_2'$ will tend to zero when $t$ tends to infinity

$$\lim_{t\to\infty} f_1' f_2' = 0. \tag{C 21}$$

For $t_0 < t < t$ the product of the increasing function $f_1'$ and the decreasing function $f_2'$ can be a decreasing function or it can have a maximum for $t_0 < t_1 < \infty$ and then tend to zero for $t \to \infty$. The maximum at time $t_1$ exists if

$$(\mathrm{d}/\mathrm{d}t)\,(\partial w/\partial w_0) = 0. \tag{C 22}$$

From (C 14) we can obtain the derivative of $\partial w/\partial w_0$ with respect to time. Equating it to zero, we get, after some transformations, the following equation

$$\frac{m}{1-m}\left[\frac{H}{K} - \left(\frac{H}{K} - w_0^{1-m}\right) \mathrm{e}^{-K(1-m)(t-t_0)}\right]^{-1} \left(w_0^{1-m} - \frac{H}{K}\right) \mathrm{e}^{-K(1-m)(t-t_0)} + 1 = 0. \tag{C 23}$$

The solution $t_1$ to (C 23) is given by

$$t_1 = \frac{1}{K(1-m)} \ln\left\{\left[1 - \left(\frac{w_0}{w_\infty}\right)^{1-m}\right] \frac{1}{1-m}\right\} + t_0, \tag{C 24}$$

where $w_\infty = (H/K)^{1/(1-m)}$ is the final body weight. To get $t_1$ greater than $t_0$, we have to assume that

$$[1-(w_0/w_\infty)^{1-m}]\,[1/(1-m)] > 1. \tag{C 25}$$

After some transformations we can see that inequality (C 25) is an equivalent to

$$(w_0/w_\infty)^{1-m} < m. \tag{C 26}$$

Thus, to sum up, the product $f'_1 f'_2$ is equal to one when $t = t_0$. If inequality (C 26) is satisfied, the product $f'_1 f'_2$ is greater than one for $t_0 < t < t_1$, it reaches a maximum at time $t_1$ and tends to zero for $t > t_1$ and $t \rightarrow \infty$. If inequality (C 26) is not satisfied, the product $f'_1 f'_2$ is less than one for $t > t_0$ and it tends to zero for $t \rightarrow \infty$. In both these cases, determined by inequality (C 26), individual weights become uniform after a sufficiently long time. If this inequality is not satisfied, the unification occurs over the whole period of growth. But if inequality (C 26) is satisfied, the differences in weights increase at first and then disappear after reaching a maximum. Inequality (C 26) is satisfied for organisms with initial weights considerably less than final weights, thus characterized by large weight increases. If we describe such growth by using the Bertalanffy or Winberg equations, then we will get uniform body weights only after the initial increase in differentiation. The coefficient $m$ occurring in the Bertalanffy equation is the exponent of the power relationship between respiration and the body weight. Bertalanffy assumed (and this is usually the case) that it is not less than 2/3. For $m = 2/3$ inequality (C 26) takes the form

$$w_0/w_\infty < 8/27. \tag{C 27}$$

This shows that it is sufficient that the final body weight be four times the initial weight for the situation described above to occur.

(3) Balance equation. It is much more difficult to find a solution to the balance equation than to the Bertalanffy equation. The weight of an individual, the growth of which is described by a balance equation, tends with time to a fixed final value given by (B 15), independent of the initial weight. This implies that weights become uniform after a sufficiently long time. Since the Bertalanffy equation is a special case of the balance equation (when $b_2 = 1$), it may be expected that the differentiation of weights with time will follow a similar pattern as in the case of the Bertalanffy equation.

(4) Model of energy flow through the organism. Such a model is a set of differential equations describing changes with time in bioenergetic parameters such as consumption, assimilation, respiration, total production, reproduction and increase in weight (Uchmański 1980*a*, 1982). Changes in the frequency distribution of calorific value (which is body weight expressed in energy units) were illustrated, for instance, on the basis of the model for energy flow through the mite *Rhizoglyphus echinopus* (Klekowski & Uchmański 1980). The equations describing energy flow through this organism were solved with the initial calorific values derived from the normal distribution. The distributions of final calorific values obtained from the simulation were also symmetric but with much lower variance. Since *R. echinopus* has an **S**-shaped growth curve (the calorific value even drops at the end of the growth period), the results obtained are consistent with what was earlier said on the other equations of limited growth.