
The effects of population density and individual diversity on time and energy budgets of animals

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Abstract: The effects of animal density, spatial heterogeneity, and diversity in individual responses to population density on daily time and energy budgets were studied by means of a simple time-energy model. The cost of interactions between individuals was expressed as a reduction of the time that an animal may spend for feeding and other activities. The value of daily production rate would decrease with the increase in density and/or in food availability. In this case, production rate would be a convex function of population density as well as of individual tolerance to the presence of other animals and the size of individual range. Therefore, under unfavourable conditions (high mean density and/or low mean food availability) both spatial heterogeneity and diversity in individual responses to the presence of neighbouring animals would lead to an increase in the mean production rate.

Keywords: Population density; Diversity; Time Budget, Energy Budget

1. Introduction

The effects of both food availability and its variability on animal's growth and energy budgets as well as the trade-off between food availability and its consumption were analyzed quite extensively (e.g., [11]; [9]; [12]; [5]; [8]; [4]. At the same time, important effects of population density and related individual variability in behavioural characteristics still are not explored so well.

In this paper we made an attempt to consider these effects from the viewpoint of the “energy-time” approach. For this purpose, we assumed that members of a population have to spend a certain time for interactions with other individuals, this time being a cost of such intra-population interactions. I also could not avoid paying attention to the joint influence of food availability and population density upon energy and time budgets. To evaluate the importance of the factors under study, we assumed that daily production rate (i.e. difference between energy assimilation and its expenditures) is to be maximised. Although daily production itself is not a direct index of fitness, it is obviously related to such characteristics as the total mass of newborn animals and/or individual growth rate. The former trait is related to fecundity and, consequently, to intrinsic population growth rate, while the latter determines size at maturity and/or longevity of maturation period. Therefore, I regarded production rate

as the first approximation to measure fitness. Any assumptions about the shape of individual growth curves were not proposed. The model is based on the general equation of energy balance (Eq.1):

$$P = A - R \quad (1)$$

where P is daily production rate, A - daily amount of assimilated energy (metabolisable energy, daily energy budget), and R is catabolised energy. All the following speculations are made under the basic assumption that $P > 0$ (daily energy balance is not negative). The following assumptions were accepted when composing the model:

(I) Daily rate of assimilation was disposed to be proportional to time spent for feeding ($\nu(F)$). This assumption, based on a good reason, underlies widely accepted concept of functional response of a consumer to resource density [3]. (II) Period of activity per day is restricted. This is obviously so for animals with expressed rhythms of activity (e.g., purely nocturnal or diurnal). Besides, the existence of an upper limit for activity period comes from physiological reasons (an animal simply is not able to be constantly active all the day round). (III) Animals were assumed to spend time first for interactions with neighboring individuals and for feeding, with the remaining part of a fixed activity period spent for other types of activity. Therefore, those populations where animals manifest tendency for interactions with each

other were regarded. Supposition (A) was formalised in the following way (Eq. 2):

$$A = \phi \cdot V(F) \quad (2)$$

where ϕ is proportion of a day, spent in feeding activity (i.e. feeding time), and $V(F)$ is an increasing function of food density F ($V'(F) > 0$). The qualitative characteristics of food (i.e. its energetic content and digestibility) were assumed to be constant. Since function $V(F)$ is supposed to be determined, then **Equation 2**, being a basic one for all the further analysis, can be solved either for ϕ or for A (**Eq. 3**):

$$\tau = \phi + \nu(N) + \beta = \text{const} \quad (3)$$

According to supposition (b), where τ is activity period (expressed as a proportion of a day), N is population density, $\nu(N)$ is density-dependent proportion of an activity period spent in interrelations between individuals (no matter either on friendly behaviour or aggressive encounters), β is proportion of a day spent in other activities. Evidently, $\nu(N)$ has to increase with the increase in population density N ($\nu'(N) > 0$). As it is shown below, I assumed that $\nu(N)$ is an increasing concave function of N ($\nu'(N) > 0$; $\nu''(N) < 0$). In the model, R formally was split into two parts [2]:

$$R = R_m + R_s \quad (4)$$

where R_m is cost of maintenance (cost of activity plus resting metabolism), and R_s is cost of production. If so, the measurable resting metabolic rate (R_r) is dependent on the productivity processes, since it consists of energy expenditures that are necessary for maintenance of the present state of an organism (B) and cost of production:

$$R_r = R_s + B \quad (5)$$

In accordance with (3), the cost of activity and maintenance of the present state of an organism is:

$$R_m = \phi \cdot (R_f - R_b) + \nu(N) \cdot (R_n - R_b) + \tau \cdot (R_b - B) + B \quad (6)$$

where R_f , R_n , and R_b -- metabolic rates during feeding, inter-individual contacts, and all the other types of activity, correspondingly. Energy expenditures for synthesis of new biomass are:

$$R_s = (1 - k) \cdot (A - R_m) \quad (7)$$

where k is the effectiveness of synthesis of new tissues ($0 < k < 1$). Then, according to (1), (4), and (7):

$$R = (1 - k) \cdot A + k \cdot R_m \quad (8)$$

and

$$P = k \cdot (A - R) \quad (9)$$

To evaluate the effects of changes in diversity (i.e. variability) of the factors under study on parameters of the time and energy budget, it is sufficient to know whether appropriate functions are convex (second derivative is positive) or concave (second derivative is negative). Increase in variability of argument leads to increase in the value of function if this is convex, and, reversibly, to its decrease in the case of concave function [4].

2. General Effects of Food Availability and Population Density

In this section following situations are modelled: (a) limitations in food intake are constant and food intake is not limited (favourable conditions), and (b): both budgets structure and total energy intake is changing (unfavourable conditions)

2.1. Changes in the Structure if Time and Energy Budgets without Changes in Total Intake of Energy (Favourable Conditions)

When population density is quite low and/or food is abundant, the condition

$$\phi + \nu(N) \leq \tau + \beta_{\min} \quad (10)$$

is correct, where is a certain minimum limit for activity, other than feeding and inter-individual contacts. Under this condition, an animal is able to keep its energy intake maximum and constant (Weiner, 1989), for it has enough time for all types of activity:

$$A = A_{\max} \quad (11)$$

where A_{\max} is a maximum possible value of daily energy intake A . According to (2) under these conditions it is ϕ that changes with changes of the value of $V(F)$:

$$\phi = \frac{A_{\max}}{V(F)}, \quad (12)$$

whereas the total energy intake is independent on both population density and food availability. Hence, the value of R_m (daily amount of energy spent for maintenance) is:

$$R_m = B + \tau \cdot (R_b - B) + \nu(N) \cdot (R_n - R_b) + \frac{A_{\max}}{V(F)} \cdot (R_f - R_b) \quad (13)$$

Since while $\phi + \nu(N) \leq \tau + \beta_{\min}$ energy intake is constant then, according to (9), productivity P would change with the increase in food and/or population density under different dependences of energetic costs of different types of activity:

If $R_f > R_b$, then productivity would increase with the

increase in food availability.

Where $R_n > R_b$ then productivity would decrease with the increase in population density.

Condition $R_b = B$ gives the situation where animals spend time only for feeding and encounters, with their actual activity period being changeable and less than a certain upper limit τ (time minimizers).

When costs of different types of activity are equal to each other ($R_f = R_b = R_n$), population density and food availability would have no effect on productivity.

When energy costs of activities, others than feeding and contacts with neighbouring individuals, are high, then the increase in food availability would decrease productivity (if $R_b > R_f$) as well as the increase in population density (if $R_b > R_n$).

2.2. Changes in Both Structures of Energy and Time Budgets and Energy Intake (Unfavourable Conditions)

All the above effects are possible if the condition (11) is correct, i.e. animals have enough time for all three types of activity – feeding, interactions with neighbouring individuals, and other actions - playing, self-care, etc ($\beta \geq \beta_{min}$). As soon as population density would exceed a certain critical value, depending on intrinsic upper limit of energy intake (A_{max}) and food abundance ($V(F)$), no possibility would remain for an animal to keep its energy intake unchanged, because feeding time would be reduced by the necessity of intra-population contacts(14):

$$\phi = \tau - \nu(N) - \beta_{max} \tag{14}$$

If so, then energy intake would increase with the increase in food availability, and decrease with the increase of time spent for intra-population contacts, since:

Simplification the situation, ($\beta_{min} = 0$) means that animals are able to spend time only for feeding and interactions with other individuals. In this case energy expenditures for maintenance would be:

$$R_m = B + \tau \cdot (R_f - B) - \nu(N) \cdot (R_f - R_n) \tag{15}$$

The response of R_m on population density would then depend on what type of activity --feeding or encounters -- is more energetically expensive. If metabolic rate during feeding is higher than this related to encounters, then the increase in time spent for encounters will be accompanied by the decrease in the total energy spending. The increase in it with growing density would be observed only if $R_n > R_f + (1/k - 1) V(F)$.

Production rate in this case is:

$$P = k \cdot (t \cdot V(F) - n(N) \cdot (V(F) - (R_f - R_n))) - R_b \tag{16}$$

For $P \geq 0$, $V(F)$ would in most cases often exceed R_f , since energy has to be at least not lower than its spending for getting food. Therefore, production rate would increase with

the increase in food availability and decrease with the increase in density both under increase or decrease in the total energy spending.

3. Shape of Time Spends for Feeding and Effects of Density and Individual Characteristics of Animals on Their Energy Budgets

For determining the shape of, $\nu(N)$ we followed logics that was used by Holling for description the I functional response of predator to pray density (Holling, 1965) If an animal spends the mean time e for each contact with other individuals, then the overall daily cost of contacts, expressed as losses of time, is

$$\nu(N) = e \cdot C \tag{17}$$

where C is the total number of encounters with other members of a population, that evidently has to increase with the increase in density. In its turn, C is apparently proportional to the time period, when an animal can meet neighboring individuals,. Since the total period of activity is restricted, then this time is equal to $\tau - \nu(N)$.

Let C be directly proportional to the population density N :

$$C = a \cdot N \cdot (\tau - e) \tag{18}$$

In this case

$$C = \frac{a \cdot N \cdot \tau}{1 + e \cdot a(N)}, \tag{19}$$

and

$$\nu(N) = \frac{e \cdot a \cdot N}{1 + e \cdot a \cdot N} \cdot \tau \tag{20}$$

Here a - coefficient of proportionality, that can be interpreted as a range of animal's activity, that is proportional to the area that is covered by an animal while moving within its home range (during a time unit). In this case, time that remains for feeding and other activities is

$$\phi + \beta = \tau - \nu(N) \tag{21}$$

Then proportion of activity other than feeding and contacts with other individuals:

$$\Omega = (\phi + \beta) - 1 \tag{22}$$

where $\Omega \in \{1, \infty\}$. Evidently, increases with the increase in the population density, in the time required for each encounter, and in the range of an animal's activity, since it is directly proportional to all these.

From (15), (21), and (22) follows that the threshold value

$\Omega = \Omega^*$
is:

$$\Omega^* = \frac{v(N)}{A_{\max}} \quad (23)$$

If $\Omega > \Omega^*$, then no time remains for any kind of activity, other than feeding and contacts with neighbouring individuals (**Fig.1**). Now for $\Omega < \Omega^*$ as it was already pointed out, R grows with the rise of Ω when $R_n > R_b$, while it decreases when $R_n < R_b$ (**Fig.2**).

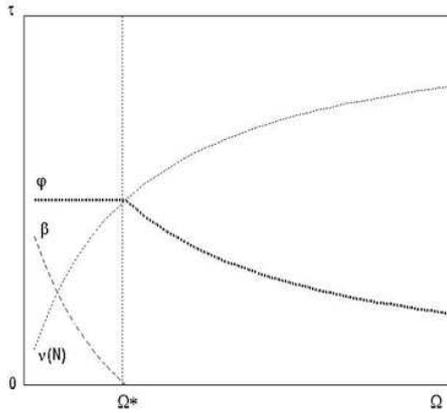


Figure 1. Dependence of time spent in different types of activity on Ω .

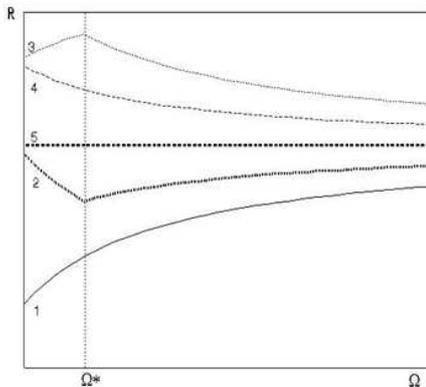


Figure 2. Dependence of the total daily energy expenditures (R) on the parameter Ω .

- (1) $R_b > R_n > R_f$;
- (2) $R_b < R_n > R_f$;
- (3) $R_f > R_n > R_b$;
- (4) $R_n < R_b < R_f$;
- (5) $R_n = R_b = R_f$.

Correspondingly, P decreases with the increase in Ω if $R_n > R_b$, and increases if $R_n < R_b$ (**Fig.3**).

For $\Omega > \Omega^*$,

$$A = \frac{V(F)}{\Omega} \quad (24)$$

When Ω passes its threshold value Ω^* , R starts to decrease with the increase of this if $R_f > R_n$ (**Fig. 2**). However, since $V(F) > R_f$, then P has to be reversibly proportional to Ω under any ratio of R_f to R_n , (**Fig. 4**). In other words, when population density exceeds its critical value, production rate of the group of animals would not only decrease with the further increase in density, but is also dependent on their individual characteristics: those animals that have broader ranges of activity and/or spend more time for one contact with other individuals would have lower production rate in comparison with the others.

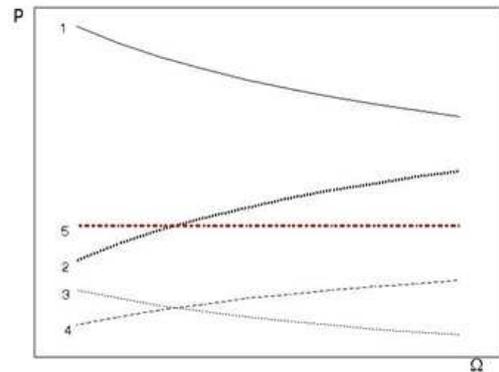


Figure 3. Dependence of the daily production (P) on the parameter Ω when food and density does not limit the total energy intake ($\Omega < \Omega^*$). Designations are the same as for figure 2.

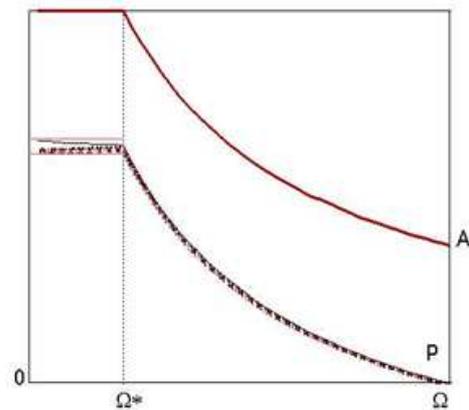


Figure 4. Dependence of the total energy intake (A) and the production rate (P) on the parameter Ω . Since this curves are concave, then diverse population composed from two separate groups (one with Ω close to Ω^*) and the other close to 1 (maximum value of W , which is an argument demonstrate higher variability of energy parameters (functions) (see [4]).

4. The Effects of Diversity in Local Density and Tolerance to other Individuals

Let us assume that exact values W are different for different individuals composing a population. This means that

either different individuals encounter different numbers of neighboring animals (due to their spatial distribution being not even and/or to their individual ranges of activity being different) or that the population *consists* of animals, some of which are more and some less tolerant to the presence of other individuals, having different values of e . Let the limits of this variability be Ω_1 and Ω_2 . If both Ω_1 and Ω_2 are lower than Ω^* , then effects of variability in responses of animals to the presence of other individuals and/or in local densities (the number of other animals within the range of the given one) are dependent on the ratio of energetic expenditures per unit of time spent in encounters (R_n) to these per unit of time spent in activities that are not related to feeding (R_b). If $R_n > R_b$, then P is a convex function of Ω , and intra-population variability leads to increase in the mean value of P . However, if $R_n < R_b$, the function is concave, and the increase in variability makes mean daily production rate to decrease.

4.1. Maximal Diversity (Simplified Situation)

Sharp dividing of a population into two separate groups with different Ω is well known that in this simplified situation (that often takes place in real populations gives high values of variability in comparison with, say, normal distribution of individuals.

Let us consider the case, when population is represented by two classes with different Ω (i.e. n_1 individuals have Ω_1 , and n_2 ; Ω_2 , and the total numbers of all individuals equal to $n_1 + n_2$. Let us also assume that energy expenditures per unit of time spent in any kind of activity are the same ($R_f = R_n = R_b$). Let now the proportion of Ω_1 -type individuals be

$$m = \frac{n_1}{n_1 + n_2} + n_2 \tag{25}$$

It is easy to show that certain value m^* exists, separating the conditions where diversity would cause either increase or decrease in the mean (population) value of P :

When $m < m^*$, diversity in Ω (i.e. spatial heterogeneity and/or co-existence of density-tolerant and density-sensitive individuals) would favour increase in energy flow through a population and total productivity under the same mean density and food availability (Fig.5)

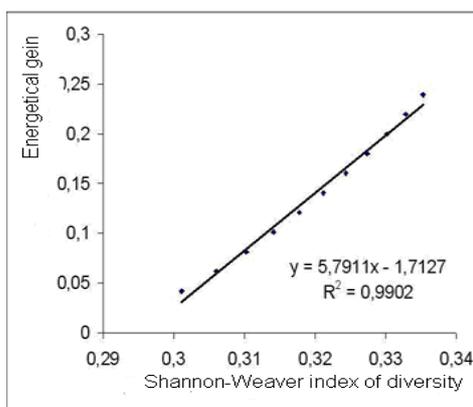


Figure 5. Dependence of energy saved due to variability of individuals on

intrapopulation diversity. This benefit is a difference between population composed by uniform individuals (no variation in their properties) and diverse population..

If both Ω_1 and Ω_2 are higher than Ω^* , then increase in variability

would lead to increase in mean P , because in this case the latter is a convex function of Ω , having positive second derivative, as it was mentioned above.

5. Discussion

In fact, intra-population competition was considered here just as an action of a certain "irritating factor", that in principle can be replaced by any other factor of this kind -- for example, by the necessity to respond to the presence of animals, belonging to other species. This factor was assumed to effect the energy budget through changes in time allocation for different types of activity. The model, based on this assumption, predicts the existence of certain threshold in both food availability and population density, where changes in time allocation start to cause changes in the total value of energy budget. The latter would decrease with the increase in density and/or with the decrease in food availability after passing this threshold by any of the above factors. In contrast to many other models describing such a response, the present model predicts that the shape of the relationship of an animal's fecundity with the population density would be different due to differences in energetic requirements for different types of behaviour.

If energy expenditures per unit of time spent in encounters exceed these for other types of activity, then the production rate would constantly decrease with the increase in density. Reversibly, if energy spending for encounters is less expensive in comparison with this for other activities, production rate would first increase with the increase of W , until it gains the maximum value (when no possibility remains for an animal to spend time for any other activity, except feeding and intra-population contacts). This leads to non-monotonous response of production rate to density, similar to that described by Allee (Allee et al., 1949).

If energetic requirements for all types of activity are equal, then a plateau would appear when the density is relatively low. Indeed, such a shape of the relationship between fecundity and population density was really observed for many species (e.g., Korytin et al., 1992).

According to the model, that is based on several very simple constructions, the time, that an animal may spend for getting food becomes to be limited by the number of other animals roaming around (population density), the size of its individual range, and the mean time that it spends for one contact with other individuals, if at least one of these characteristics exceeds a certain threshold, depending on extrinsic factors (e.g., food availability). The corresponding dependence would be described as

(1) a convex function. As a consequence, assimilation and production

(2) rates would also be convex functions of the above pa-

rameters.

Such a circumstance gave a base for making conclusions about the role of individual variability in the mean value of production rate for a group of individuals (i.e. mean fecundity of a population). It is worth mentioning also that, in terms of the proposed model, decrease in production rate caused by the increase in density would lead to corresponding decrease in the observed resting (or basal, under the thermo-neutral conditions) metabolism R_r (Eq. 5). For instance, this was observed in experiments with artificially increased density of rodents under laboratory conditions, especially in individuals of low hierarchical rank [10]; [7]. In terms of the model, the animals that have higher e (i.e. paying more attention to the presence of other individuals), would have lower R_r in comparison with others. Therefore, the joint effect of density and hierarchical rank of animals on their resting metabolic rate are described here in terms of time and energy budgets.

However, further development of the model is needed to make any conclusions about the influence of factors under study on the population growth (that requires incorporation of mortality that may be both density-dependent and tolerance-dependent) and individual growth (that requires consideration the process in the course of time, in contrast to the "snapshot" treated here). For instance, it was shown that environmental variability would be either maximized or minimized in dependence on the shape of growth curve as well as in dependence on what parameter is to be maximized: maturation time or size on reproduction (Houston, McNamara, 1990).

6. Conclusions

The main conclusion is that under high mean density and/or low food availability, the patchiness in spatial distribution, the variability of individual ranges, and the diversity in individual responses to density would be favourable for a population in sense of increase of production rate. In other words, the model predicts that under unfavourable conditions the population composed of individuals, different in their tolerance to population density, with their ranges being of different size, and distributed unevenly through the territory, would produce more offspring than the population composed by evenly distributed and uniform animals. Therefore, co-existence of "density-tolerant" (e is low) and "density-intolerant" individuals (e is high) as well as "residents" (a is low) and "dispersers" (a is high) under relatively high population density and/or under insufficient food supply can be explained in terms of time-energy approach as a mechanism, promoting the increase in the current production rate of the whole population. However, if environmental

conditions are not so severe (mean value of Ω is less than a critical level or close to it), homogeneity sometimes may be more favourable than heterogeneity, in dependence with the ratio of energetic costs of different types of activity.

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