First Notes for the Implementation of a DEB Model for the Ñandú (Rhea americana)

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Motivation

Dynamic Energy Budget (DEB) theory aims to quantify the energetics of individuals as it changes during life history. The key processes are feeding, digestion, storage, maintenance, growth, development, reproduction and aging.

Knowledge of intake and use of energy by wild fauna may be used for modifying this energy flux with maximum efficiency in order to raise strategies for conservation and management. Thus, a *Dynamic Energy Budget (DEB) model* may be used for optimizing the population dynamics of a wild species by optimizing the individual catabolic processes.

Introduction

Rheas are found only in South America, where there are two species: *Rhea americana* and *Pterocnemia pennata*. For the first species, there are three subspecies recognized: *Rhea americana americana, Rhea americana intermedia* and *Rhea americana albescens*. *Rhea americana americana* is the native flightless bird that inhabits the grasslands of province of Buenos Aires. **1**

There are two main reasons for modelling this species. On the one hand, the population of *ñandúes* has decreased considerably. A reason for this is the development of agriculture, because producers tend to exterminate it because it harms the crops and because they believe it competes with cattle for grass. On the other hand, this species has been exploited traditionally to take advantage of its meat and their feathers, but nowadays, when farming producers are considering to increase their trade on the international markets, they must face the problem of the conservation of the species.

In this situation, the *DEB* model might be introduced as a tool for the modelling of the energy requirements being indispensable for a successful reproduction.

 1 After reading the textbook, we think this "sub-speciation" might be related to the different latitudes, because the individuals present geographical size variations and they tend to be bigger towards the South Pole.

Biological Data

Rheas are large herbivores similar to African ostriches. They may stand 1.3-1.8 *m* tall and they may weigh 25-38 *kg*. Their body is mainly ovoid and it is covered with large feathers. Their wings are well developed for courtship and aggressive display, but they can not fly. Their legs are long and strong, well adapted for running.

In the wild, their life-span is about fifteen years. They reach their maximum body size around the first year and the reproductive maturity when they are two years old.

They combine polygyny (one male mates with more than one female) and polyandry (one female mates with more than one male). The striking feature of their reproductive behaviour is the dominant role of the male, who performs courtship displays, builds the nest (a depression in the ground), incubates the eggs, and rears the young, whereas the female is limited to mating and egg lying.

In late September, when the breeding season starts, the dominant male monopolizes a harem of females which lay eggs communally in a single nest and later the male incubates them for 37- 45 days.

The DEB Model for the Ñandú

Basic Points

Ñandúes are:

- heterotrophs (they obtain the nutrients they need to live by consuming other organisms);
- endotherms (their body heat is regulated by internal physiological mechanisms);
- isomorphs (the individuals conserve their shape as they growth in size);

Their life pattern presents three stages: embryo, juvenile (divided in two "sub-stages") and adult (divided in two sub-stages, too).

The transition from embryo to juvenile is given by the start of food intake and the juvenile to adult one is given by the start of the energy allocation for reproduction.

In view of the lack of information about the growth of Rheas, this model can be stated in two different ways. If we consider Rheas as bang-bang strategist (their growth ceases after attaining certain puberty volume V_p), we should distinguish two sub-stages in the juvenile stage, because *ñandúes* do not allocate any energy for reproduction until their growth ceased *(Juvenile I*). In the next sub-stage, they start to allocate energy for reproduction but they are not able to reproduce yet *(Juvenile II)*. If we consider them as constant-fraction-strategist (they allocate a constant fraction of catabolic energy to somatic maintenance plus growth during all life stages), we should consider only one juvenile stage.

Furthermore, we differentiate between adults who are able to reproduce *(Adults I)* and non-productive adults due to aging processes *(Adults II)*.

Structuring the model also in sexes is relevant because the reproduction costs are different for males than for females depending on each sub-stage.

For the sake of completitude, the model might include seasonal changes such as food abundance, rainfall, etc.

Energy Acquisition and Use

The *DEB model* is built considering two state variables: reserves *(E)* and structural biomass *(V)*. The different processes which together constitute this model are roughly summarized in *Figure 1*, where the relationship among those processes is chosen by following the fate of food.

Figure 1: Processes in the DEB Model

Ingestion Process

In wild habitats, *ñandúes* feed on green plants (graminoids, cool season grasses, warm season grasses, forbs and legumes). Nevertheless, *ñandú* chicks eat insects too, and throughout the reproductive season, adults consume small amounts of animal material (small insects, small bone fragments), presumably ingested for incorporating more protein and calcium.

Food enters a thin-walled, glandular stomach (proventriculus) and then a muscular gizzard (ventriculus).

For isomorphs, the ingestion rate is:

$$
\dot{\bm{J}}_{X} = {\{\bm{J}_{X_{m}}}\} f \, V^{2/3}
$$

where:

 ${J_{X_m}} = \frac{X_m}{V^2}$ *m X* X_m ^{$J - V$} *J* J_{X_m} } = $\frac{X_m}{\sqrt{2}}$ *m* \dot{r} J_{X_m} } = $\frac{J_{X_m}}{I_Z}$: surface-area-specific maximum ingestion rate, measured in grams (for

the sake of simplicity) per day per squared metres;

f : scaled functional response, dimensionless;

V : structural body volume, measured in cubic metres.

Because there are no quantitative studies on the diet of *ñandúes* in the wild (all the studies about diet are qualitative and referred only to botanical composition), we are going to use an empirical datum. Available information on adults in a management ranch tells that they are fed daily with 750 grams (dry matter) of *alfalfa (Medicago sativa)*. Thus, we consider $\dot{J}_{X_m} = 750$ *g/d* and $f = 1$ (abundant food condition); for the maximum structural body area, $V_m^{2/3}$, we assume the approximate value of 0.60 m^2 ². Hence, the surface-area-specific maximum ingestion rate yields $\{\dot{J}_{X_m}\}=1.25\cdot10^3$ $g/(m^2d)$ and the ingestion rate (measured in grams per day) becomes:

$$
J_{X} = 1.25 \cdot 10^{3} \text{ V}^{2/3}
$$

Assimilation Process

The term "assimilated energy" denotes the free energy fixed into reserves. It equals the intake minus free energy in all losses related to digestion (faeces included). Thus the assimilation rate is proportional to the ingestion rate:

$$
\dot{p}_A = \{p_{A_m}\}fV^{2/3} = \frac{\{p_{A_m}\}}{\{J_{X_m}\}}\{J_{X_m}\}fV^{2/3}
$$

where:

 $\{\dot{p}_{A_m}\} = \frac{1}{\sqrt{2/3}}$ *m m A* A_m ^{*f*} $-\frac{V}{V}$ *p p* 'n \dot{p}_{A_m} } = $\frac{P_{A_m}}{V^{2/3}}$: surface-area-specific maximum assimilation rate, measured in

kilojoules per squared meter per day;

f, V: as before.

Because the value for \dot{p}_{A_m} could not be obtained in the literature, we attempted to estimate it by knowing: a) the total metabolizable energy of the *alfalfa* consumed by the individual and b) the field metabolic rate for *ñandú (FMR)*.

² This structural maximum area was estimated by adding the areas of neck and head, body and legs (fingers included). Indeed, this is a very rough first approximation, obtained from measurements of skins.

a) Metabolizable Energy of *Alfalfa*

The metabolizable energy *(ME)* of each component of a plant species (crude protein, *CP*; fat, *FA*; dietary fiber, *DF*; nitrogen-free extract, *NFE*) is calculated by multiplying the energy per gram of that component in the species (in kilojoules per gram) by the amount of the component in plant tissue (in grams per kilogram of dry matter). For ruminants (Williams *et al.*, 1993) **3** , the *ME* in plants components is 12 *kJ/g* for *CP*, 31 *kJ/g* for *FA*, 5 *kJ/g* for *DF*, and 14 *kJ/g* for *NFE*.

The total *ME* of *alfalfa*, 10149 kilojoules per kilogram of dry plant tissue, was obtained by adding the energy contents of the four components in it (see *Table 1*). Then, the *ME* of 750 *g* of *alfalfa* (dry matter) is 7612 *kJ*.

Table 1: Nutrient Analysis of Alfalfa (Estación Experimental Agropecuaria INTA Rafaela)

b) Field Metabolic Rate for *Ñandú*

FMR is the total daily energy cost of a wild animal. It includes basic metabolism rate (the minimum energy its body requires to maintain basic functions such as respiration and circulation, regardless of the activity), thermoregulation, movement, feeding, digestion, growth, reproduction and other expenditures that eventually ends up as heat production (Nagy, 1987).

Values for this rate could not be found but Williams *et al.* (1993) propose the following allometric function for the *FMR* of "all" birds **4** :

$$
M_F = 9.57 \, w^{0.689}
$$

where:

l

 M_F : FMR, measured in kilojoule per day; *w* : body mass, measured in grams.

The calculated value for *ñandúes* (using a mean weight of 31,5 *kg*) was 12030 *kJ/d*. Then, if we compare these requirements with the total metabolizable energy in 750 *g* of alfalfa, we noticed this ration is not enough to satisfy their needs. It is only enough for covering their BMR

³Williams *et al.* justify this approximation because, in contrast to other herbivores, ostriches accrue a substantial proportion of their energy needs from microbial fermentation and, like ruminants, they retain digesta for long periods.

⁴ For adult ostriches, this equation does not provide an accurate estimate of *FMR* (26% lower than predicted); however, it is a good approximation for sub-adults (8% lower than predicted). We think it might be a good estimate for *ñandúes*, because their weights are comparable and thus the error can be roughly estimated.

of 3968 *kJ/d*, estimated by using the following allometric function (Grawford & Lasiewski, 1968):

$$
M_B = 78.3 \, w^{0.723}
$$

and the same weight. 5

We can conclude that these individuals are eating other organic material in addition to the supplied *alfalfa* (probably, wild grass); in a different way, the minimum amount of ingested alfalfa should be near 1.20 kilograms. Another acceptable reason for the discrepancy might be the calculation of the *ME* of *alfalfa* by using data for ruminants.

Finally, we must say that this unexpected result (obtained on the very rough assumption that all metabolizable energy in the plant was assimilated by the individuals) does not allow us to estimate the maximum assimilation rate for *ñandúes*. In this manner, we can only suggest, as another rough first approximation, the use of common values of digestibility of *alfalfa* for ruminants (about 65%) as an upper boundary for this rate. Thus, we were able to calculate the surface-area-specific maximum assimilation rate as $\{\dot{p}_{A_m}\}=8.25\cdot 10^3 kJ/(m^2d)$ by considering an assimilation of 65% of the energy contained in the maximum amount of alfalfa that an individual can ingest. Consequently, the assimilation rate (measured in kilojoules per squared metre per day) becomes:

$$
p_A = 8.25 \cdot 10^3 \, V^{2/3}
$$

and the conversion efficiency of food into assimilated energy can be written as:

$$
\frac{\{p_{A_m}\}}{\{J_{X_m}\}} = \frac{8.25 \cdot 10^3 \, kJ/(m^2 d)}{1.25 \cdot 10^3 \, g/(m^2 d)} = 6.60 \, kJ/g
$$

Reserve Dynamics

As a very good approximation, the dynamics of the reserves can be expressed trough the following equation:

$$
\frac{d}{dt}E = \dot{p}_A - \dot{p}_C
$$

⁵ In spite of the fact that allometric functions are usually more descriptive than explanatory and hence problematic, they constitute the little information available.

where:

E : non-allocated energy in reserves;

 p_A : energy flux (power) of process of assimilation; i. e., assimilated energy;

 \dot{p}_c : energy flux (power) of process of catabolism, i. e., energy consumed by the body tissues.

The " κ -rule" suggests a fixed proportion κ of energy utilised from the reserves is spent on growth plus maintenance and the remaining portion *(1–*κ) is spent on development and reproduction. Maintenance and growth compete directly, while development and reproduction compete with growth plus maintenance at a higher level. If conditions are poor, the system can block allocation to reproduction while maintenance and growth continue to compete in the same way.

In the case of *ñandúes* we could not to estimate the dynamics of their reserves because of the lack of information about the energy flux of each process.

The single available information about energy requirements of *Ratites* is referred to ostriches and it is given by behaviour (sitting, standing, walking, pecking, preening, others) and not by process (maintenance, growth, maturity, reproduction). (Williams *et al.*, 1993).

Structural Volume Dynamics

The dynamics of the structural volume can be written as:

$$
\frac{d}{dt}V = \frac{\kappa \dot{p}_c - \dot{p}_M - \dot{p}_T}{[E_G]}
$$

where:

 \dot{p}_M : energy flux (power) of process of maintenance, i.e., maintenance costs;

 p_T : energy flux (power) of process of heating, i.e., heating costs;

 $[E_G]$: volume-specific growth costs.

When we attempted to determine the structural volume dynamics of *ñandúes*, we found out the same troubles discussed in *Reserve Dynamics* and we could not perform this task.

Conclusions

In order to develop a complex model such as this one for *Rhea americana*, it is necessary to perform a lot of research about their physiological processes and their energy requirements. If finding out a simple relation between behaviours and processes could be possible, the data of Williams *et al.* (1993) for ostriches might be used as a very rough first approximation for

ñandúes. Afterwards, the model could be used for study their growth when different diets are considered.

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