Predicting post-natal energy intake of lesser black-backed gull chicks by Dynamic Energy Budget modeling

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ABSTRACT

The standard Dynamic Energy Budget (DEB) model is widely used to describe the physiology of individual animals. Here we parametrized the DEB model for the lesser black-backed gull *Larus fuscus* mainly on the basis of literature data. Next we performed an inverse modeling approach to predict the food intake rate of gull chicks (model input) on the basis of their growth trajectory from hatching to fledging (model output). Food intake rate and growth were also measured for this period in an aviary experiment, where three different diet treatments resulted in a large range in overall intake rate. These measured food intake rate data were not used in the parameter estimation procedure, but rather to validate model results. Model predictions of food intake rate were systematically only about 10% below the observations, but predictions and observations correlated strongly. The DEB model might be used to predict food provisioning rates in the field, which are difficult to obtain, on the basis of growth data, which are much easier to get.

1. Introduction

In vertebrate species with parental food-provisioning, post-natal growth of the young strongly depends upon the amount of food that the parents are able to deliver. If food availability or parental effort is insufficient, the newborns may show reduced growth rates and even starve to death, with negative effects on the population renewal rate. For a deeper understanding of the dynamics of such populations in relation to the abundance of their prey, one therefore needs to know both the link between food availability and provisioning rate, and the link between food intake rate and growth rate of the young. Measuring the provisioning or intake rate in the field is, however, a laborious and costly exercise.

Here we examine whether the Dynamic Energy Budget (DEB) model is capable of predicting the food intake rate of the young on the basis of their growth trajectory. One might call this an inverse modeling exercise, as the model input (food intake rate) is predicted from the model output (growth rate). The dynamic energy budget (DEB) theory, developed by Kooijman (2010), is the most comprehensive theory that links the food environment to the major physiological processes of individual organisms, such as feeding, growth, and reproduction. The

inclusion of reserves acting as metabolic memory, the full-life cycle of individuals (embryo, juvenile, adult) and the explicit use of conservation laws (energy, chemical elements and isotopes) sets the DEB theory apart from other approaches.

The standard DEB model can already be parametrized for a particular species on the basis of a very restricted data set. A set of data that contains only eight so-called zero-variate data and one so-called univariate data set already suffices for estimating the 8 most important DEB parameters (Lika et al., 2014). A feasible zero-variate data set might include, for example, age at birth, age at first reproduction, lifespan, weight at birth, weight at first reproduction, maximum weight, maximum length, and maximum reproduction rate. Weight at age data is an example of a useful univariate data set. Over the last few years a wealth of published (see, for example, Marques et al. (2018); van der Meer et al. (2014) and references therein) and unpublished (compiled at https:www.bio.vu.nl/thb/deb) parameter estimations of the DEB model were done for a rapidly growing number of species. This collection of species, which comes under the name of the add_my_pet collection has presently about 2500 entries, including over 400 different bird species.

DEB theory provides an integrated look at whole-organism

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energetics and it is therefore possible to predict specific process rates without ever having measured these rates. This sets this mechanistic and theory-based modeling approach apart from a statistical approach, e.g. by fitting allometric relationships, which is still prevalent in most ecological research. One previous example of the strength of the DEB approach is the case of the Atlantic hagfish *Myxine glutinosa*, a species that has no otoliths, which makes aging them impossible. It furthermore tends to behave abnormally in captivity, as it, for example, refuses to eat, and growth and reproduction rates can not be obtained in the laboratory either. Data on oxygen consumption versus weight were, however, available, and this allowed the estimation of growth rates and age at maturity by using DEB modeling (van der Meer and Kooijman, 2014). A major though inevitable shortcoming of the exercise was that the predictions could not be tested, as true data on hagfish growth rates were not available. Other examples of DEB predictions are food intake reconstructions on the basis of growth trajectories for emperor penguins *Aptenodytes forsteri* (Kooijman, 1993) and for various bivalve and fish species (Cardoso et al., 2006; Freitas et al., 2009; Jusup et al., 2014; Kooijman, 1993; Lavaud et al., 2019; Pecquerie et al., 2012; Troost et al., 2010). Most of these studies suffered from the same shortcoming that food intake predictions could not be tested, with the exception of Jusup et al. (2014) who were able to correlate predicted and measured annual food intake for captive bluefin tuna.

Here we present another food intake reconstruction study in which DEB predictions are tested. For this, we use data of an aviary experiment where food intake rate of lesser black-backed gull *Larus fuscus* chicks was manipulated and precisely measured for almost the entire growth period of the chicks. Additionally, the growth response was measured. We first estimate the parameters of the standard DEB model for the lesser black-backed gull using a limited data set mainly gathered from the open literature. Next we apply an inverse modeling approach to predict the food intake rate over the entire growth period for all experimental chicks on the basis of their observed growth patterns (mass versus age). Hence we do not use any feeding data in fitting the DEB model parameters. Finally, we compare model predictions to true measurements of food intake.

As measuring growth of bird chicks in the field is much easier than measuring food intake rate during the entire growth period, the inverse modeling approach, as applied here, is of practical use for field ornithologists to predict the required overall food intake for obtaining a specific fledging weight.

2. DEB modelling

Below we will give a very short introduction to the standard DEB model for the individual organism. A more extensive introduction is given in the Appendix, but we refer the reader also to Kooijman (2010) for a detailed description of underlying DEB assumptions and derivations, or to van der Meer (2006, 2016, 2019), who provides easier accessible introductions.

The model organism has three succeeding life stages, the embryo, which neither feeds nor reproduces, the juvenile, which feeds but does not reproduce, and the adult, which feeds and reproduces. The organism is described by three state variables: (1) structural body volume, (2) reserve density, which is the amount of reserves per unit of structural body volume, and (3) maturity, which is the cumulative energy allocated to development. Embryos and juveniles develop, i.e. build up maturity. Transitions between embryo and juvenile and between juvenile and adult occur at fixed levels of maturity. Once the animal has become adult, it has reached its maximum maturity and starts to reproduce. The present application focuses on changes in the structural body volume and reserve density of the juvenile stage.

The standard DEB model can be entirely re-written in a dimensionless form, meaning that all state variables and time are scaled by some quantity that has the same physical dimension as the original variable. For example, structural body length (the cubic root of structural body volume) is scaled by maximum body length. Such scaling has the advantage that the equations look much simpler, and the dynamical behavior of the system of coupled differential equations can be more easily studied without any loss of generality. The dynamics of the scaled reserve density e in scaled time τ are given by

$$\frac{de}{d\tau} = \frac{f - e}{l} \tag{1}$$

where f is the so-called scaled functional response that relates the assimilation rate to the food density, and takes a value between zero (no food) and one (ad libitum). Note that food density is the only environmental variable. The variable l stands for scaled length. Growth is given by the differential equation for scaled length

$$\frac{dl}{d\tau} = \frac{1}{e + g} \frac{e - l}{3} \tag{2}$$

where the compound parameter g is called the 'energy investment ratio'. It stands for the energetic costs of new structural volume relative to the maximum energy within the reserves that is available for growth and maintenance. See the Appendix for further details about the scaling procedure.

3. Parameter estimation

The DEB parameter estimation procedure starts with 8 so-called zero-variate data points and 6 pseudo-data points (Table 1). These pseudo-data are in fact standard values for a selection of DEB parameters and these values are taken from Kooijman (2010), Table 8.1. There are theoretical reasons to expect that the values of these parameters are invariant among species Kooijman (2010). The pseudo-data are used in the fitting procedure to avoid non-convergence problems, and resemble the use of priors in Bayesian analysis. The procedure further uses one so-called univariate data set, i.e. body weight obtained at a various ages.

Zero-variate data on length and mass at birth and at first reproduction, on maximum reproductive rate and on maximum length and mass are all taken from published or unpublished work by Camphuysen (see Table 2 for references). The assumed maximum age of 34 years and 10 months is based on the EURING list of longevity records for European birds (Fransson et al., 2017). Maximum age only affects the estimate for the Weibull aging acceleration parameter $\dot{h}_a$, whose value is irrelevant for the present exercise. Hence the precise

Table 1

Data used to fit the standard Dynamic Energy Budget model. Data in the upper part of the table are true zero-variate data, the middle part gives pseudo-data. These pseudo-data are a-priori estimates of the parameters and might be needed to avoid overfitting. The lower part gives true univariate data. The last column gives the model equations that link the data to the model parameters; L_∞ is the ultimate structural body length, δ_M the shape coefficient. Section (Sn) and equation (Eq) numbers refer to Kooijman (2010).

Variable	Explanation	Model
a_b	Age at birth	Sn 6.1.1
t_X	Time since birth at fledging	
t_R	Time since birth at first brood	
a_m	Life span	Sn 6.1.1
$L_{w,\infty}$	Ultimate physical length	L_∞ / δ_M
W_b	Wet mass at birth	Sns 1.2.3, 2.6.2; Eq. 3.2
W_p	Wet mass at first brood	Sns 1.2.3, 2.6.2; Eq. 3.2
W_∞	Ultimate wet mass	Sns 1.2.3, 3.2.1; Eq. 3.2
$\dot{R}_\infty$	Ultimate reproductive rate	Eq. 2.58
$\dot{v}$	Energy conductance	
κ	Allocation fraction to soma	
$[\dot{p}_M]$	Volume-specific somatic maintenance rate	
κ_G	Growth efficiency	
W_w, t_X	Wet mass versus time since birth	Sns 1.2.3, 3.2.1; Eq. 3.2

Table 2
Observed versus predicted zero-variate data for the lesser black-backed gull. Data in the upper part of the table are true data, the lower part gives pseudo-data. Weight refers to the weighing of the squared relative differences in the optimization procedure. Egg development occurs at a temperature of 6 ˚C, after hatching body temperature equals 41.2 ˚C, whereas the pseudo-data are given for a reference temperature of 20 ˚C.

Variable	Observed	Predicted	Unit	Weight	Source
a_b	29	29	d	1	Camphuysen (2013)
t_x	37	37.52	d	1	Camphuysen (2013)
t_R	1095	562	d	1	Camphuysen (2013)
a_m	12714	12720	d	1	Fransson et al. (2017)
$W_{w, b}$	55.32	55.23	g	1	Camphuysen (2013)
$W_{w, R}$	1065	1092	g	1	Camphuysen (2013)
$W_{w, \infty}$	1065	1091	g	20	Camphuysen (2013)
L_∞	55	55.01	cm	1	Camphuysen (2013)
$\dot{R}_m$	0.008219	0.008191	d^{-1}	1	Camphuysen (2013)
$\dot{v}$	0.02	0.3801	cmd^{-1}	0.004	Kooijman (2010)
κ	0.8	0.9499	-	0.2	Kooijman (2010)
$[\dot{p}_M]$	18	244.8	$Jd^{-1}cm^{-3}$	0.1	Kooijman (2010)
κ_G	0.8	0.8005	-	1	Kooijman (2010)

maximum age value does not matter here. The univariate data on wet weight versus age are the only data that were taken from the aviary experiment (see below). For each day the maximum observed wet weight was taken.

The standard DEB model provides predictions for all data. We do not repeat the relevant equations that have been used to provide these predictions, but refer the reader to Kooijman (2010). Detailed references to the equations are given in Table 1. For completeness, several conversion coefficients should be mentioned here: wet mass-volume 1 g per cm^3, dry mass-volume 0.28 g per cm^3, energy per C-mole in the reserves 550 kJ per C-mole (Kooijman, 2010), and dry mass 23.9 g per C-mole (Kooijman, 2010). Combined these coefficients reveal an energy content within the reserves of 3.9 kJ per gram wet mass.

DEB model parameters are estimated according to a procedure described by Lika et al. (2011) and Marques et al. (2018). Not all parameters were estimable, and we have chosen to set the estimates for a few parameters at predefined values (Table 3), taken from Table 8.1 from Kooijman (2010). The goodness-of-fit function that is minimized in the procedure by Lika et al. (2011) is a weighted sum of squares. Apart from the symmetric mean squared error (SMSE), the mean

Table 3
Parameter estimates of the standard Dynamic Energy Budget model for the lesser black-backed gull. All rates are given for a reference temperature T_{ref} of 293 K. Parameter values printed in italics were set at a predefined value that was taken from Kooijman (2010), Table 8.1.

Parameter	Value	Unit	Explanation
T_A	*9000*	K	Arrhenius temperature
f	*1*	-	Scaled functional response
δ_M	0.1517	-	Shape parameter
t_0	22.97	d	Time at start development
$\{\dot{p}_{Am}\}$	2150.6	$Jd^{-1}cm^{-2}$	Area-specific assimilation rate
$\dot{v}$	0.3801	cmd^{-1}	Energy conductance
κ	0.9499	-	Allocation fraction to soma
κ_X	*0.8*	-	Assimilation efficiency
κ_{Xp}	*0.1*	-	Faeces efficiency
κ_R	*0.95*	-	Reproduction efficiency
$[\dot{p}_M]$	244.8	$Jd^{-1}cm^{-3}$	Volume-specific somatic maintenance rate
$\dot{k}_J$	*0.002*	d^{-1}	Maturity maintenance rate coefficient
$[E_G]$	7318	Jcm^{-3}	Specific costs for structure
E_{Hb}	1590	J	Maturity at birth
E_{Hx}	888900	J	Maturity at fledging
E_{Hp}	3.493e6	J	Maturity at puberty
$\dot{h}_a$	1.327e-29	d^{-1}	Weibull aging acceleration
s_G	*0.01*	-	Gompertz stress coefficient

relative error (MRE) is also reported, see Lika et al. (2011) and Marques et al. (2018) for details. We have chosen to put more emphasis on the univariate data and on data on maximum weight and maximum feeding rate. The DEB model routines and the parameter estimation routine are part of the software packages DEBtool and Add-my-pet and can be downloaded from the Theoretical Biology website of the VU University Amsterdam https://www.bio.vu.nl/thb/deb

4. Aviary experiment

Data from a previously published aviary experiment are used (Gupta et al., 2016). Forty eggs of lesser black-backed gull were collected from the wild in 2015 and taken to the Wildlife Rescue Centre in Oostende, Belgium. The eggs were incubated and after hatching randomly assigned to one of four diet treatment groups. Here we use data from three treatments. The first is called terrestrial, and contains 80% terrestrial food plus 20% marine food. It was called S1 in Gupta et al. (2016). The second is called marine, previously named S2, and contains 20% terrestrial plus 80% marine food. The last one is called mixed, and contains 50% of both types of food. This treatment was not discussed in Gupta et al. (2016). All marine (consisting of cod *Gadus morhua*, mackerel *Scomber scombrus* and whiting *Merlangius merlangus*) and terrestrial food items (mealworm larva *Tenebrio molitor*, potato crisp and broiler chicken *Gallus gallus domesticus*) were homogenised, mixed and embedded in gelatine to avoid selective feeding. Gelatine contributed 20% of total pellet dry weight. Food pellets were offered in an unrestricted amount and food taken was measured on a daily basis. The total time until fledging was split up in periods of 3-5 days. Length and weight measurements were done at the end of each period. For further details we refer to Gupta et al. (2016).

5. Inverse modeling

The standard DEB model was simulated for each bird separately. The initial value of scaled structural length for the first observational period was derived from the observed physical length. Initial scaled reserve density for this first period was set to 1, which means that unscaled reserved density is equal to the maximum reserve density, i.e. to the ratio $\{\dot{p}_{Am}\}/\dot{v}$. The model was subsequently run for a series of scaled functional response f values. The f value that 'exactly' predicted the observed physical length at the end of each observation period, was selected. A quadratic function between f and physical length was used for interpolation. The predicted physical length and reserve density at the end of the period were used as initial values for the next observation period. This way the length predictions exactly followed the observations.

6. Results

The aviary experiment showed that food intake rates in terms of energy per time were highest for those birds feeding on terrestrial food and lowest for those that were restricted to marine food (Fig. 1). A similar difference was observed in the growth trajectories (Fig. 2). The mixed diet took an intermediate position in both food intake and growth rates.

Parameter estimation resulted in a fit with a symmetric mean squared error (SMSE) of 0.141, and a mean relative error (MRE) of 0.066. Compared to other species, these goodness of fit measures pointed to a good fit, see the add-my-pet website https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/about.html for an overview. All predictions for zero-variate data were close to observations, except for time since birth at first brood (Table 2). Observed time at first brood is three years (1095 days), but the prediction equaled only 562 days. This discrepancy is usually observed for birds, where the actual age of first breeding seems to be merely determined by behavioral constraints and not so much by physiological ones. The fitted growth trajectory, making
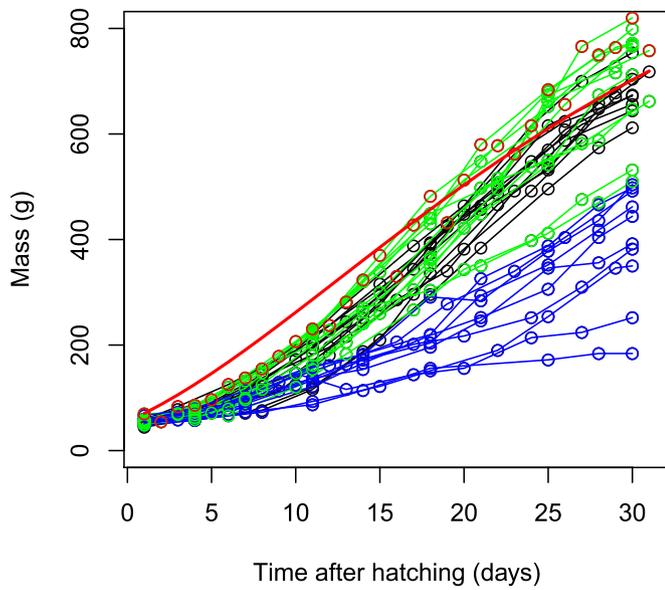
Fig. 1. Food intake versus time after hatching. Green dots and lines for a terrestrial diet, black for mixed and blue for marine.
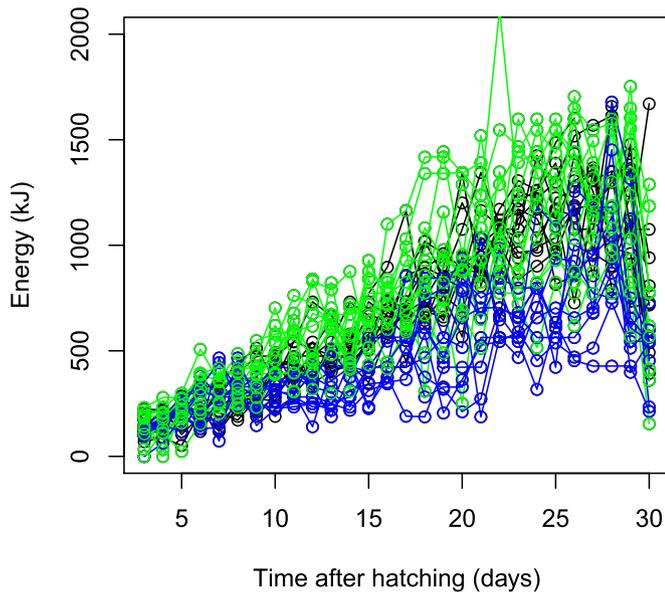

Fig. 2. Wet mass versus time after hatching for lesser black-backed gulls fed with three different diets. The red dots give the maxima per day and the red line gives the DEB prediction at *ad libitum* food. Green dots and lines for a terrestrial diet, black for mixed and blue for marine.

Fig. 3. Relative food level, as expressed by the scaled functional response f, versus observation period. Green dots for a terrestrial diet, black for mixed and blue for marine.
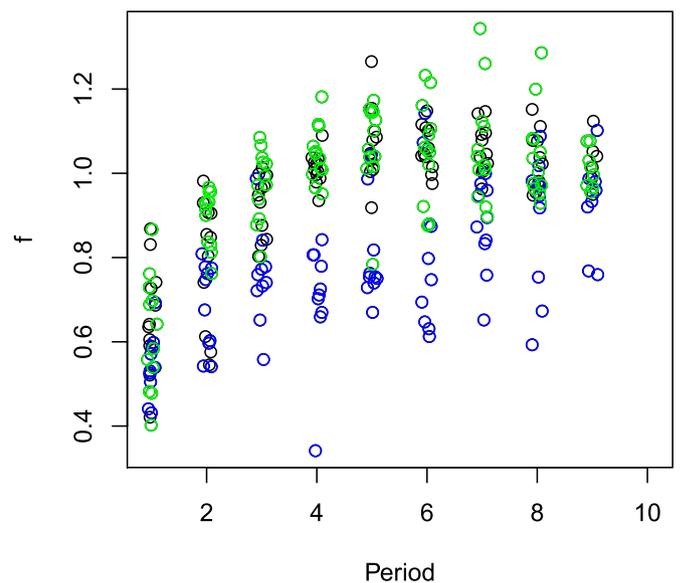
Fig. 4. Wet mass versus time after hatching for a particular individual (upper panel), predicted food intake rate per day and observed food intake rate per day (middle panel), predicted scaled reserve density (lower panel).

the assumption that the scaled functional response equaled 1 for the entire growth period, initially overestimated the mass of the birds (Fig. 2). This observation is also in line with that for other bird species. The parameter estimates (Table 3) also agree with those for other bird species (Teixeira, 2016).

The inverse modeling also pointed to a lower intake rate during the first few periods than the maximum achievable, even for the terrestrial treatment. After these initial periods the scaled functional response varied around 1 for the terrestrial treatment, slightly lower for the mixed, and around 0.7 for the marine treatment (Fig. 3).

Fig. 4 shows, as an example, the results of the inverse modeling for one haphazardly chosen bird that obtained a mixed diet. The growth curve fits of course exactly through the data, as the scaled functional response f is fitted for each period separately (Fig. 4, upper panel). The predicted daily food intake followed the observations remarkably well
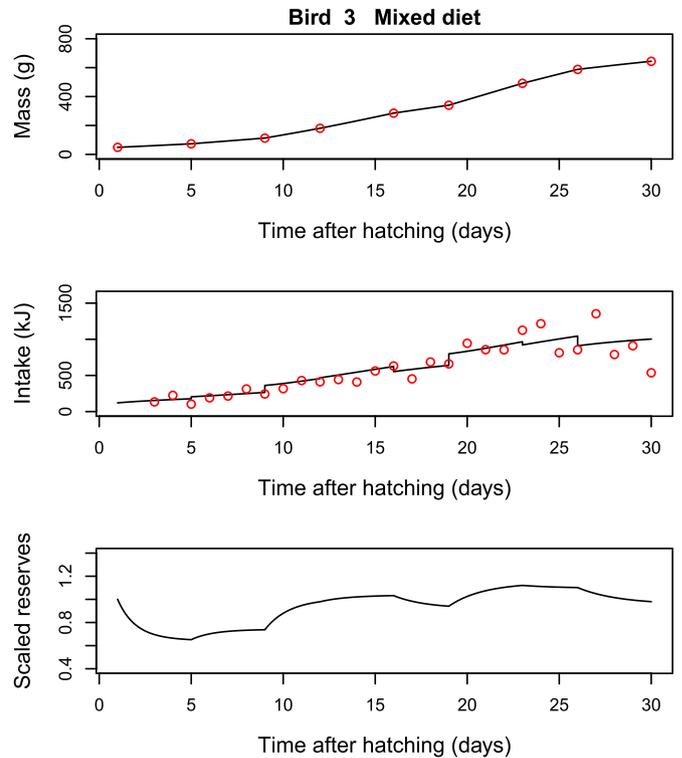
(Fig. 4, middle panel). The scaled reserve density follows the scaled functional response with some delay (Fig. 4, lower panel). Plots for other birds are not shown, but revealed similar goodness of fits. Overall the measured food intake was about 10% higher than the predicted intake (Fig. 5).

7. Discussion

A major goal in ecology is to understand how fitness-related

Fig. 5. Predicted versus observed food intake, as measured over the first 30 days after hatching. Green dots for a terrestrial diet, black for mixed and blue for marine.

Fig. 6. Predicted food intake over the first 30 days after hatching versus mass at the age of 30 days after hatching. Green dots for a terrestrial diet, black for mixed and blue for marine.

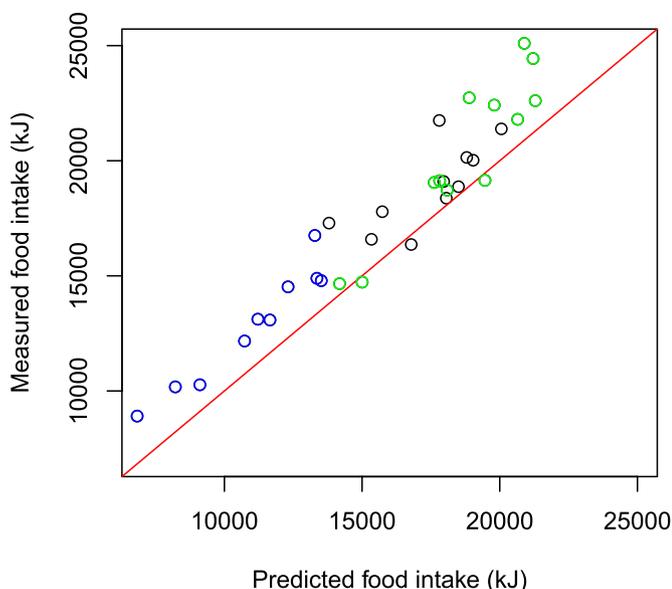performance of organisms responds to the environment. The availability of food is without doubt one of the most crucial environmental variables. It is therefore not surprising that numerous studies have been performed, though mainly in the laboratory, to determine the functional response that relates food availability to food intake rate, and to estimate the parameters of the appropriate type of functional response model (Jeschke et al., 2002). Much less attention has, however, been paid to study the next step, that is the relation between food intake rate and fitness-related characteristics such as growth rate, reproduction rate and survival. A likely reason for this discrepancy in research attention is that functional response experiments can be performed over relatively short time periods, i.e. for most species trials of minutes to hours will suffice, whereas studies of the link between food intake rate and growth or reproduction ideally last for the entire growth or reproductive period, which may take weeks to years.

Measuring food intake is, as already said, a laborious and costly exercise, particularly in the field. It is therefore encouraging that the modeling approach based on DEB theory, as presented here, enables a rather accurate prediction of food intake rate of the chicks on the basis of their growth trajectory, or simply on basis of their mass 30 days after hatching (Fig. 6). This enables ornithologists to study the functional response (i.e the link between food availability and food gathering rate) in the field in probably the most important period of the year, that is in the chick raising period. Provisioning rate, or at least intake rate of the chicks can now directly be derived from the growth trajectory of the chicks, which is much easier to obtain. Of course, feeding rate of the adults themselves has to be added to obtain the total food gathering rate. Adult feeding rate can be obtained in a similar fashion, if changes in adult weight are available. These weights will probably only vary to a minor extent, implying that adult feeding rate is more or less constant.

In our experiment differences in food intake rate, and thus in scaled functional response, were not directly related to differences in density of the same type of food, but to differences in food quality. One might question why those birds fed with a marine diet, that apparently has low energy density, simply do not eat more? It could be that they are already at the limit of total mass intake rate (van Gils et al., 2005).

Apart from predicting the intake rate required for obtaining a specific fledging weight, the DEB model keeps track of all energy fluxes. The huge difference in weight increase as a result of a much smaller difference in food availability ($f = 1$ versus $f = 0.7$), is not just the
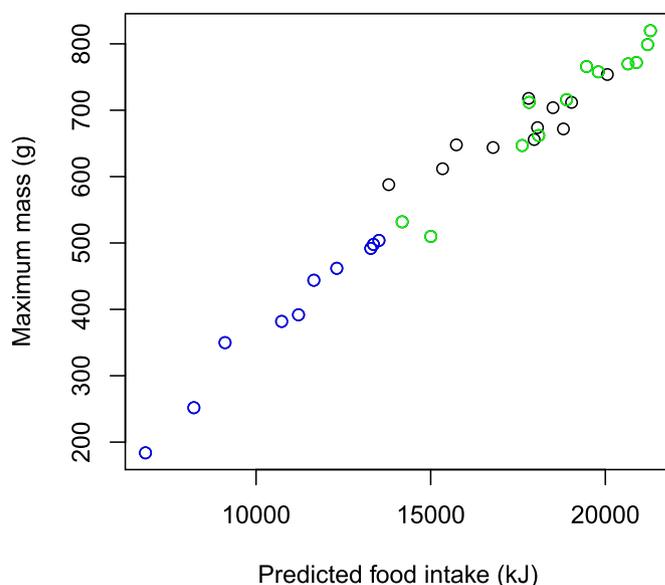
Table 4
Various energy expenditures (kJ), that is powers integrated over the first 30 days after hatching, predicted by the standard DEB model for abundant ($f = 1$) and limited ($f = 0.7$) food. Maturity includes maturity maintenance.

Type	Integral	$f = 1$	$f = 0.7$
Feeding	$\int \dot{p}_X \, da$	19717	8891
Assimilation	$\int \dot{p}_A \, da$	15774	7113
Mobilization	$\int \dot{p}_C \, da$	13973	6682
Maintenance	$\int \dot{p}_M \, da$	10943	5530
Growth	$\int \dot{p}_G \, da$	2329	817
Maturity	$\int \dot{p}_J \, da$	700	335

Table 5
State variables of the standard DEB model and environmental variables. L stands for the dimension length of the structural body, e for energy, # for mass measured in terms of C-moles, and l for the dimension length of the environment.

Symbol	Dimension	Interpretation
V	L^3	Structural body volume
$[E]$	eL^{-3}	Reserve density
E_H	e	Maturity
T	T	Temperature
X	$\#l^{-3}$	Food density in the environment

result of the difference in structural size but also to a great extent of the difference in reserves (Table 4). Note that the build-up of the reserves is given by the integrated assimilation minus the integrated mobilization, and thus equals 1801 kJ and 431 kJ for the two example feeding levels. This difference is relatively larger than that in structural growth: 2329 kJ versus 817 kJ.

Our food intake predictions were systematically about 10% below the observations. We refrained from using these food intake data in the parameter estimation procedure, but when we would have done that, it would have resulted in an almost perfect fit. Lowering the assimilation efficiency (which was set at 80%) would as well have yielded such perfection. A slightly lower efficiency of 75% has indeed been observed in birds (Castro et al., 1989). The slow initial growth observed might also be related to a low initial assimilation rate, similar to a lowered

digestive performance after diet switching (Hilton et al., 2000). It may be that the newly hatched chick needs a few days to get adapted to feeding itself. Chicks are initially poorly able to keep themselves warm, which may have added thermoregulation costs. But probably this played no role, as the chicks were under a heat lamp during the first three days.

Generally speaking, the problem of overfitting (too many parameters, too few data types) is always a serious one, particularly in such complex parameter estimation procedures as the add-my-pet procedure for DEB models. Testing the predictions of a parametrized model on an independent data set, as was done here, is therefore of utmost importance in modeling. We strongly encourage such tests for DEB models. As a next step, it might be rewarding to repeat our exercise for a variety of bird species for which data on intake rate during the chick raising phase are available.

Author Contributions

AS and LL designed the feeding experiments; JvdM and SvD fitted the DEB model to the data; JvdM developed and applied the inverse modeling procedure; JvdM wrote the manuscript, with the help of SvD. All authors contributed to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Appendix A

This appendix provides further details and derivations for the standard DEB model. The model has three state variables, structural body volume V, reserve density $[E] = E/V$, which is the amount of reserves per unit of structural body volume, and maturity E_H, which is the cumulative energy allocated to development. The most important environmental variable is the food density X (Table 5).

A list of assumptions give rise to a set of coupled ordinary differential equation for the three state variables. Assumptions for the standard DEB model are, among other things, that (1) assimilation rate is proportional to the surface area of the structural body $\dot{p}_A = \{\dot{p}_{Am}\}fV^{2/3}$, (2) all assimilated energy enters the reserves and is then mobilized from the reserves (the rate of changes of the reserves is thus the difference between the assimilation rate and the mobilization rate), (3) a fixed fraction κ of the mobilization rate is spent on maintenance, which is assumed proportional to structural body volume, and on growth, assuming fixed costs for growth per unit volume, (4) the rate of change of maturity equals $1 - \kappa$ times the mobilization rate minus the maturity maintenance costs, which are proportional to maturity.

The ordinary differential equation for reserve density is

$$\frac{\mathrm{d}[E]}{\mathrm{d}t} = V^{-1/3}(\{\dot{p}_{Am}\}f - \dot{v}[E]) \tag{3}$$

The area-specific assimilation rate $\{\dot{p}_{Am}\}$ and the energy conductance $\dot{v}$ are so-called primary parameters of the standard DEB model. They are explained, together with quite a few others such as $\{\dot{F}_m\}$ and κ_X, in Table 6; f is the so-called scaled functional response that relates the assimilation rate to the food density, and is given by

$$f = \frac{X}{\frac{\{\dot{p}_{Am}\}}{\{\dot{F}_m\}\mu_X\kappa_X} + X}$$

and μ_X is the chemical potential of the food.

The growth equation is given by

$$\frac{\mathrm{d}V}{\mathrm{d}t} = \frac{\kappa\dot{v}[E]V^{2/3} - [\dot{p}_M]V}{\kappa[E] + [E_G]} \tag{4}$$

Table 6
Primary parameters of the standard DEB model. See further Table 5.

Symbol	Dimension	Interpretation	Process
$\{\dot{p}_{Am}\}$	$eL^{-2}t^{-1}$	Surface-area-specific maximum assimilation rate	Assimilation
$\{\dot{F}_m\}$	$l^3L^{-2}t^{-1}$	Surface-area-specific searching rate	Feeding
κ_X	-	Digestion efficiency	Digestion
$\dot{v}$	Lt^{-1}	Energy conductance	Mobilisation
κ	-	Fraction of mobilisation rate spent on maintenance plus growth	Allocation
$[\dot{p}_M]$	$eL^{-3}t^{-1}$	Volume-specific maintenance rate	Turnover/activity
$\{\dot{p}_T\}$	$eL^{-2}t^{-1}$	Surface-area-specific maintenance rate	Heating/osmosis
$[E_G]$	eL^{-3}	Volume-specific costs of growth	Growth
$\dot{k}_J$	-	Specific maturity maintenance	Regulation/defence
κ_R	-	Reproduction efficiency	Egg formation
E_H^b	e	Maturity at birth	Life history
E_H^p	e	Maturity at puberty	Life history

It follows from

$$\frac{dE}{dt} = \frac{d[E]V}{dt} = \dot{p}_A - \dot{p}_C \tag{5}$$

which tells that the rate of changes of the reserves is the difference between the assimilation rate $\dot{p}_A$ and the mobilization rate $\dot{p}_C$. A fraction κ of the mobilization rate is spent on maintenance, which is assumed proportional to structural body volume, and on growth, assuming fixed costs for growth per unit volume. Using this so-called κ-rule and the product rule for differentiation, Eq. 5 can be re-written as

$$V\frac{d[E]}{dt} + [E]\frac{dV}{dt} = \{\dot{p}_{Am}\}fV^{2/3} - \frac{1}{\kappa}[\dot{p}_M]V - \frac{1}{\kappa}[E_G]\frac{dV}{dt}$$

Combining with Eq. 3 and some re-arranging yields the growth Eq. 4.

The rate of change of maturity equals $1 - \kappa$ times the mobilization rate minus the maturity maintenance costs, which are proportional to maturity. Hence

$$\frac{dE_H}{dt} = (1 - \kappa)\dot{p}_C - \dot{k}_J E_H \tag{6}$$

for $E_H < E_H^p$. Else, that is when the animals have become mature and $E_H = E_H^p$, maturity does not change anymore and $dE_H/dt = 0$.

It can be shown that the mobilization rate $\dot{p}_C$ equals

$$\dot{p}_C = \frac{[E]}{\kappa[E] + [E_G]}(\dot{v}[E_G]V^{2/3} + [\dot{p}_M]V)$$

The system of differential equations for reserve density (Eq. 3), structural volume (Eq. 4), and maturity (Eq. 6) describe the standard DEB model.

The standard DEB model can be entirely re-written in a dimensionless form. In order to arrive at a dimensionless model one has to re-scale all dimensions, that is energy, length (or volume) and time. The choice of scaling coefficients is rather arbitrary, as we will see. Yet, for energy an obvious choice is the maximum amount of energy in reserve E_m, and for volume it is the maximum volume of the structural body $V_m = (\kappa\{\dot{p}_{Am}\}/[\dot{p}_M])^3$. The maximum amount of energy in reserve equals the product of the maximum reserve density and the maximum volume $E_m = [E_m]V_m$, where $[E_m] = \{\dot{p}_{Am}\}/\dot{v}$ as follows from eqn. 3 with $f = 1$. These choices ensure that the new dimensionless state variables, which are scaled reserve density $e \equiv [E]/[E_m]$ and scaled length $l \equiv (V/V_m)^{1/3}$ are easy to interpret and to remember. The same holds for scaled maturity $e_H \equiv E_H/E_m$. The choice of a scaling coefficient for time is less obvious. But it helps to first look at power, which is given in energy per time. One option is to scale power by the maximum assimilation rate, which equals $\dot{p}_{Am} = \{\dot{p}_{Am}\}V_m^{2/3}$. This choice implies that time is scaled to κ times the ratio of the maximum reserve density and the volume-specific maintenance rate, resulting in $\tau \equiv t[\dot{p}_M]/(\kappa[E_m])$.

Not just the state variables, but all parameters (Table 7) and model equations can now be re-scaled. Eq. 3, which describes the dynamics of the reserve density, turns into

$$\frac{de}{d\tau} = \frac{d[E]}{dt}\frac{1}{[E_m]}\frac{\kappa[E_m]}{[\dot{p}_M]} = \frac{f - e}{l} \tag{7}$$

Similarly, the growth Eq. 4 becomes

$$\frac{dl^3}{d\tau} = \frac{dV}{dt}\frac{1}{V_m}\frac{\kappa[E_m]}{[\dot{p}_M]} = \frac{1}{e + g}l^2(e - l) \tag{8}$$

which is equivalent ($\frac{dl^3}{d\tau} = \frac{dl^3}{dl}\frac{dl}{d\tau} = 3l^2\frac{dl}{d\tau}$) to

$$\frac{dl}{d\tau} = \frac{1}{e + g}\frac{e - l}{3} \tag{9}$$

where the compound parameter g is given by the ratio $[E_G]/(\kappa[E_m])$. This is one of the most important compound parameters in DEB theory and is called the 'energy investment ratio'. It stands for the energetic costs of new structural volume $[E_G]$ relative to the maximum available energy for growth and maintenance $\kappa[E_m]$.

Eq. 6 can be re-written as

Table 7
Rescaling the primary parameters of the standard DEB model written in an energy-length framework into a dimensionless framework. Energy is scaled to the maximum energy in reserves $[E_m]V_m$, volume to the maximum volume V_m, and power to the maximum assimilation rate $\{\dot{p}_{Am}\}V_m^{2/3}$. Hence time is scaled to one over the product of the energy investment ratio and the maintenance rate coefficient $(g\dot{k}_M)^{-1}$.

Energy-length	Dimension	Dimensionless
$\{\dot{p}_{Am}\}$	$eL^{-2}t^{-1}$	1
$\dot{v}$	Lt^{-1}	1
$[\dot{p}_M]$	$eL^{-3}t^{-1}$	κ
$\{\dot{p}_T\}$	$eL^{-2}t^{-1}$	κl_T
$[E_G]$	eL^{-3}	κg
E_H^b	e	e_H^b
E_H^p	e	e_H^p

$$\frac{\mathrm{d}e_H}{\mathrm{d}\tau} = \frac{\mathrm{d}E_H}{\mathrm{d}t} \frac{1}{[E_m]V_m} \frac{\kappa[E_m]}{[\dot{p}_M]} =$$

$$(1 - \kappa)l^2 \frac{e}{e + g}(g + l) - \frac{\dot{k}_J}{\dot{k}_M g}e_H$$

(10)

where the compound parameter $\dot{k}_M$, called the 'maintenance rate coefficient' is given by the ratio $[\dot{p}_M]/[E_G]$. It stands for the maintenance costs of structure relative to the investment. When $\dot{k}_J = \dot{k}_M$, which means that the relative maintenance costs of maturity equal those of the somatic body, it can be shown that

$$E_H = \frac{1 - \kappa}{\kappa}[E_G]V$$

or, in dimensionless form, $e_H = (1 - \kappa)gl^3$. The main result of setting $\dot{k}_J = \dot{k}_M$ is thus that maturity occurs at a fixed length, that is $e_H^p = (1 - \kappa)gl_p^3$. The consequence is that Eq. 10 simplifies to

$$\frac{\mathrm{d}e_H}{\mathrm{d}\tau} = (1 - \kappa)\left(\frac{e}{e + g}l^2(g + l) - l^3\right)$$

(11)

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