**Energy budget model structure and patterns**

## Parameters:

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Submodel | Symbol | Value | Code | Description [units] (reference) | Source |
| **EI** |  | 5.07 | stomach-fill-perc | Stomach fill as percent body mass [%] | Meese 1971 |
| **EI** |  | 83.6 | AE-food | Assimilation efficiency of food [%] | Piątkowska & Weiner 1987; Kaczmarski 1966; Meese 1971; Peacock and Speakman 2001 |
| **EI** |  | 22.8 | HIF | Heat increment of feeding [%] | Hastings et al. 1997; Even and Blais 2016 |
| **EI** |  | 67 | DM-food | Dry matter content of foodstuffs [%] | Meese 1971 |
| **EI** |  | 12281.1 | ED-food | Energy density of foodstuffs [J g-1 wet mass] | Meese 1971 |
| **M** |  | 6053.1 | B0 | Normalization constant [unitless] | Sadowska et al. 2015; Grosiak et al. 2020; Górecki 1968 |
| **M** | γ | 0.64 | gamma | Allometric scaling exponent [unitless] | Sadowska et al. 2015; Grosiak et al. 2020; Górecki 1968 |
| **COT** |  | 0.166 | speed-mean | Mean movement velocity [m s-1] | Maiti et al. 2019 |
| **COT** |  | 0.822 | speed-max | Maximum movement velocity [m s-1] | Maiti et al. 2019 |
| **COT** |  | 4.7 | intercept-pcot | Intercept of the postural cost function [J 30min-1] | Chappell et al. 2004; Dlugosz et al. 2009; Rezende et al. 2006 |
| **COT** |  | 0.63 | slope-pcot | Slope of the postural cost function [unitless] | Chappell et al. 2004; Dlugosz et al. 2009; Rezende et al. 2006 |
| **COT** |  | 10.6 | intercept-icot | Intercept of the incremental cost of transport function [J kg-1 m-1] | Pontzer 2016 |
| **COT** |  | -0.29 | slope-icot | Slope of the incremental cost of transport function [unitless] | Pontzer 2016 |
| **R** |  | 20 | t-gest | Gestation time [days] | Koivula et al. 2003; Bujalska & Ryszkowski 1966; Kaczmarski 1966 |
| **R** |  | 4 | t-0 | Implantation delay for lactating females [days] | Brambell and Rowlands 1936; Bujalska & Ryszkowski 1966; |
| **R** |  | [2, 9] | n-emb-range | Range of number of conceived embryos [N] | Brambell and Rowlands 1936, Nerquaye-Tetteh and Clarke 1990, Nyholm and Meurling 1979, & Wiger 1979 |
| **R** |  | 21 | t-nurs | Nursing time [days] | Kaczmarski 1966; Oksanen et al. 2001; Oksanen et al. 1999; Horne & Ylönen 1998 |
| **R** |  | 620 | t-max-age | Maximum age [days] | Buchalczyk 1970; Rudolf et al. 2017; Sawicka-Kapusta 1974; Balčiauskienė 2007 |
| **R** |  | [30, 45] | t-mature | Age of female maturity [days] | Oksanen et al. 2001; Bujalska 1983; Buchalczyk 1970 |
| **R** |  | [121, 273] | t-mating | Mating days [day of year] | Oksanen et al. 2001; Koivula et al. 2003; Nyholm & Meurling 1975 |
| **R** |  | 0.112 | emb-growth-c | Fetal growth constant [day-1] | Ożdżeński and Mystkowska 1976 |
| **R** |  | 6.910-8 | emb-mass-init | Fetal mass at conception [g] | Ożdżeński and Mystkowska 1976 |
| **R** |  | 19.957 | emb-mass-inf | Asymptotic fetal mass [g] | Ożdżeński and Mystkowska 1976 |
| **R** |  | 3.8 | percent-fat-emb | Fetal body composition-Fat [%] | Fedyk 1974; Sawicka-Kapusta 1974 |
| **R** |  | 10.2 | percent-pro-emb | Fetal body composition-Protein [%] | Fedyk 1974; Sawicka-Kapusta 1974 |
| **R** |  | 3,249.9 | ED-pl | Energy density of placental tissue [J g-1] | Luz and Griggio 1996 |
| **R** |  | 50.1 | DE-pl | Deposition efficiency of placental tissue [%] | Greizerstein 1982 |
| **R** |  | - | preg-prob-const | Logistic pregnancy investment steepness constant [unitless] | Calibrated |
| **R** |  | - | preg-prob-mid | Logistic pregnancy investment logistic midpoint [unitless] | Calibrated |
| **R** |  | 50.1 | off-BMR-red | Relative offspring basal costs multiplier [%] | Kam, Khokhlova and Degen 2006; Koteja and Weiner 1993 |
| **R** |  | 88.0 | off-growth-eff | Efficiency of offspring growth [%] | Kam and Degen 1993 |
| **R** |  | 82.5 | milk-prod-eff | Efficiency of producing milk from body stores [%] | Bondi 1982; Romero et al. 1975 |
| **R** |  | - | lact-prob-const | Logistic lactation investment steepness constant [unitless] | Calibrated |
| **R** |  | - | lact-prob-mid | Logistic lactation investment logistic midpoint [unitless] | Calibrated |
| **LM** |  | 23.5 | ED-pro | Protein energy density [kJ g-1] | Fedyk 1974; Livesey 1984; Brody 1968; Kleiber 1975 |
| **LM** |  | 73.5 | DE-fat | Deposition efficiency of fat [%] | Pullar and Webster 1977 |
| **LM** |  | 44.4 | DE-pro | Deposition efficiency of protein [%] | Pullar and Webster 1977 |
| **LM** |  | - | growth-lm-prob-const | Logistic lean mass deposition investment steepness constant [unitless] | Calibrated |
| **LM** |  | - | growth-lm-prob-mid | Logistic lean mass deposition investment logistic midpoint [unitless] | Calibrated |
| **LM** |  | 0.0264 ± 0.0011 | growth-lm-inf | Asymptotic lean mass [kg] | Fedyk 1974; Hansson 1991; Rudolf et al. 2017; Sawicka-Kapusta 1974; Balčiauskienė 2007; Gębczyński 1975 |
| **LM** |  | 0.0964 ± 0.0155 | growth-lm-k | Lean mass growth constant [day-1] | Fedyk 1974; Hansson 1991; Rudolf et al. 2017; Sawicka-Kapusta 1974; Balčiauskienė 2007; Gębczyński 1975 |
| **S** |  | 39.1 | ED-fat | Fat energy density [kJ g-1] | Fedyk 1974; Livesey 1984; Brody 1968 |
| **S** |  | 19.1 | EC-pro | Energy density of catabolized protein [kJ g-1] | Brody 1968; Kleiber 1975 |
| **S** |  | 0.015 | gamma-mobilize | Fuel partitioning constant [Unitless] | Belkhou et al. 1991; Dunn et al. 1982; Cherel et al. 1992 |
| **S** |  | 11.9 | percent-water-adi | Water percent in adipose tissue [%] | DiGirolamo and Owens 1976; Reinoso et al. 1997 |
| **S** |  | 39.8 | max-SL | Maximum storage level [%] | Maximum fat percentage in Fedyk 1974 – as estimated as the maximum value +1SD adjusted for water content |
| **D** |  | - | surv-prob-const | Logistic survival probability steepness constant [unitless] | Calibrated |
| **D** |  | - | surv-prob-mid | Logistic survival probability logistic midpoint [unitless] | Calibrated |
| **D** |  | - | surv-mod-emb | Embryo survival probability modifier [unitless] | Calibrated |
| **D** |  | - | surv-mod-off | Offspring survival probability modifier [unitless] | Calibrated |
| **D** |  | 28.8 [20.0, 63.2] | winter-surv | Female mean overwinter survival probability (range in brackets) [%] | Koskela, 1998; Oksanen et al. 2001; Kallio et al. 2007; Boratyński et al. 2010; Haapakoski et al 2012 |

## Equations:

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Submodel | Function [units] | Code | Symbol | Equation | Source |
| **EI** | Stomach fill modifier [%/100] | stomach-mod |  |  | - |
| **EI** | Stomach clear rate [30min-1] | stomach-clear-rate |  |  | Abraham et al. 2021 (base equation) |
| **EI** | Maximum stomach fill [g] | stomach-fill-max |  |  | - |
| **EI** | Total potential ingestion rate for a timestep [g] | IR-timestep |  |  | Hopkins and Blundell 2017 |
| **EI** | Scaled storage level from -1 to 1 [unitless] | SL-scaled |  |  | - |
| **EI** | Ingestion rate modifier based on scaled storage level [%] | IR-mod |  |  | Based on Speakman 2014 |
| **EI** | Record of unmet food requirements [g] | food-debt |  |  | Gallagher et al. 2021 |
| **EI** | Ingestion rate [g 30min-1] | IR-real |  |  | Gallagher et al. 2021 |
| **EI** | Realized ingestion rate adjusted for stomach fill [g 30min-1] | IR-real |  |  | - |
| **EI** | Update record of unmet food requirements [g] | food-debt |  |  | Gallagher et al. 2021 |
| **EI** | Metabolizable energy intake [J 30min-1] | MEI |  |  | - |
| **EI** | Heat of increment of feeding [J 30min-1] | m-HIF |  |  | - |
| **EI** | Assimilated energy [J 30min-1] | energy-assimilated |  |  | - |
| **M** | Maintenance costs [J 30min-1] | m-BMR |  |  | Kleiber 1975; Sibly et al. 2013 |
| **COT** | Probability of moving based on energy balance [%] | move-prob |  |  | - |
| **COT** | Cost of transport [J 30min-1] | m-move |  |  | Pontzer 2016; Chappell et al 2013; Halsey 2013; Molnár et al. 2010 |
| *Pregnancy* | | | | | |
| **R** | Fetal growth rate [g 30min-1] | max-growth-emb |  |  | Ricklefs 2010 |
| **R** | Fetal tissue investment [J 30min-1] | m-growth- emb |  |  | Boult et al. 2018 |
| **R** | Placental growth rate [g 30min-1] | max-growth-pl |  |  | Mu et al. 2008 |
| **R** | Placental tissue investment [J 30min-1] | m-growth-pl |  |  | - |
| **R** | Allocation to pregnancy based on storage level [%] | perc-allo-preg |  |  | Desforges et al. 2020 |
| **R** | Total cost of pregnancy [J 30min-1] | m-preg |  |  | - |
| **R** | Update embryo mass [kg] | mass-emb |  |  | - |
| **R** | Update placental mass [kg] | mass-pl |  |  | - |
| **R** | Update gestational mass [kg] | gest-mass |  |  | - |
| *Lactation* | | | | | |
| **R** | Offspring maintenance costs [J 30min -1] | m-BMR-off |  |  | Kleiber 1975; Sibly et al. 2013 |
| **R** | Offspring growth rate [g 30min-1] | max-growth-off |  |  | Sibly et al. 2013 |
| **R** | Offspring lean mass protein content [%] | lean-mass-perc-pro |  |  | Fedyk 1974; Sawicka-Kapusta 1974 |
| **R** | Energy density of lean mass [J kg-1] | ED-lean-mass |  |  | - |
| **R** | Offspring costs of lean mass growth [J 30min -1] | m-growth-lm-off |  |  | Boult et al. 2018 |
| **R** | Allocation to lactation based on storage level [%] | perc-allo-lact |  |  | - |
| **R** | Total cost of lactation [J 30min -1] | m-lact |  |  | Kam et al. 2004 |
| **LM** | Lean mass protein content [%] | lean-mass-perc-pro |  |  | Fedyk 1974; Sawicka-Kapusta 1974 |
| **LM** | Energy density of lean mass [J kg-1] | ED-lean-mass |  |  | - |
| **LM** | Allocation to lean mass deposition based on storage level [%] | perc-allo-growth-lm |  |  |  |
| **LM** | Lean mass deposition rate [kg 30min-1] | lean-mass-depo |  |  | Sibly et al. 2013 |
| **LM** | Cost of lean mass deposition [J 30min -1] | m-lean-mass |  |  | Boult et al. 2018 |
| **-** | Total costs [J 30min -1] | m-tot |  |  | - |
| **S** | Protein contribution to storage dynamics [%] | protein-storage-perc |  |  | Caloin 2004 |
| **S** | Adipose synthesized [kg 30min -1] | adipose-synthesized |  |  | - |
| **S** | Lean mass synthesized [J 30min -1] | lean-mass-synthesized-energy |  |  | - |
| **S** | Reserve mobilization from adipose tissue [kg 30min -1] | adipose-mobilized |  |  | - |
| **S** | Energy mobilization from lean mass [J 30min -1] | lean-mass-mobilized-energy |  |  | - |
| **S** | Energy flux from lean mass [J 30min -1] | e-diff |  |  | - |
| **S** | Realized lean mass flux [kg 30min -1] | lean-mass-change |  |  | - |
| **S** | Update lean mass [kg] | lean-mass |  |  | - |
| **S** | Update adipose mass [kg] | adipose-mass |  |  | - |
| **S** | Update total mass [kg] | mass |  |  | - |
| **S** | Update storage level [kg] | storage-level |  |  | - |
| **D** | Survival probability [%] | surv-prob |  |  | Nabe-Nielsen et al. 2018; Desforges et al. 2020 |
| **D** | Embryo survival probability [%] | surv-prob-emb |  |  | - |
| **D** | Offspring survival probability [%] | surv-prob-off |  |  | - |

## State variables:

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Symbol | Code | | Description [units] | |
| ***Agent state variables:*** | | | | |
|  | mass | | Mass [kg] | |
|  | lean-mass | | Mass of lean (non-adipose) tissues [kg] | |
|  | adipose-mass | | Mass of adipose tissues [kg] | |
|  | age | | Age in days [days] | |
|  | storage-level | | Storage level (adipose stores as a percentage of mass) [%] | |
|  | pregnancy-status | | Pregnancy status [true or false] | |
|  | lactation-status | | Lactation status [true or false] | |
|  | m-BMR | | Basal metabolic rate [J 30min-1] | |
|  | m-move | | Metabolic cost of transport [J 30min-1] | |
|  | m-growth | | Metabolic cost of growth\* [J 30min-1] | |
|  | move-speed | | Movement speed [m 30min-1] | |
|  | energy-assimilated | | Energy from food resources [J] | |
|  | energy-mobilized | | Energy from mobilized tissues [J] | |
|  | ITV-BMR | | Individual trait variation in basal metabolic rate [%] | |
|  | ITV-growth | | Individual trait variation in allocation to lean mass growth [%] | |
| *For pregnant or lactating females:* | | | | |
|  | n-emb | | Number of embryos [N] | |
|  | mass-emb | | Mass of embryo [kg] | |
|  | gest-mass | | Gestational mass (combined mass of embryos and placentae) [kg] | |
|  | m-growth-emb | | Metabolic cost of growth of embryo [J 30min-1] | |
|  | m-preg | | Metabolic cost of pregnancy [J 30min-1] | |
|  | ds-mating | | Days since mating [days] | |
|  | n-off | | Number of offspring [N] | |
|  | mass-off | | Mass of dependent offspring [kg] | |
|  | SL-off | | Storage level of offspring (adipose stores as a percentage of mass) [%] | |
|  | lean-mass-off | | Lean mass of dependent offspring [kg] | |
|  | sex-off | | Sex of dependent offspring [“male” or “female”] | |
|  | m-BMR-off | | Basal metabolic rate of dependent offspring [J 30min-1] | |
|  | m-growth-LM-off | | Metabolic cost of lean mass growth of lactating offspring [J 30min-1] | |
|  | m-lact | | Metabolic cost of lactation [J 30min-1] | |
|  | ds-birth | | Days since giving birth [days] | |
|  | ITV-repro | | Individual trait variation in allocation to reproduction [%] | |
| ***Environmental state variables:*** | | | | |
|  | | resource-level | | Food resource level of a patch [g] |

## Patterns:

**For calibration:**

1. Fetal mass at birth

2. Birth mass by litter size

3. Total body mass by age

4. Lean mass by age

5. Lactating mother mass by pup age

6. Lactating mother food intake by pup age

7. Total litter mass by pup age

8. Mother peak food intake by litter size

9. Mother peak energy use by litter size

10. Mother peak milk transfer by litter size

11. Pup mass at weaning by litter size

12. Litter size at birth

13. Litter size at weaning

14. Probability of weaning by mother body mass

15. Average / range of body fat %

16. Body fat % of living animals

17. Field metabolic rate by body mass

**For evaluation:**

18. State-dependent field metabolic rate

19. State-dependent food consumption

20. Survival rates

21. Age-class structure

22. Local population densities