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Title:

sOAR: A tool for modelling optimal animal life-history strategies in cyclic environments

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Abstract

Periodic environments determine the life cycle of many animals across the globe and the timing of important life history events, such as reproduction and migration. These adaptive behavioural strategies are complex and can only be fully understood (and predicted) within the framework of natural selection in which species adopt evolutionary stable strategies. We present sOAR, a powerful and user-friendly implementation of the well-established framework of optimal annual routine modelling. It allows determining optimal animal life history strategies under cyclic environmental conditions using stochastic dynamic programming. It further includes the simulation of population dynamics under the optimal strategy. sOAR provides an important tool for theoretical studies on the behavioural and evolutionary ecology of animals. It is especially suited for studying bird migration. In particular, we integrated options to differentiate between costs of active and passive flight into the optimal annual routine modelling framework, as well as options to consider periodic wind conditions affecting flight energetics. We provide an illustrative example of sOAR where food supply in the wintering habitat of migratory birds significantly alters the optimal timing of migration. sOAR helps improving our understanding of how complex behaviours evolve and how behavioural decisions are constrained by internal and external factors experienced by the animal. Such knowledge is crucial for anticipating potential species' response to global environmental change.

Keywords

State variable model, life history theory, stochastic dynamic programming (SDP), optimal annual routine model (OAR/ARM), full annual cycle model (FAC), trade-offs, fitness, annual cycle

Introduction

Life on earth is subject to various geophysical cycles such as the solar day or the seasons (Numata and Helm 2014). In response to these cycles, many animals display rhythmic patterns of behaviour (Numata and Helm 2014). For example, migratory birds respond to seasonal environments by undertaking regular long-distance journeys between breeding and wintering habitat (Alerstam 1990). Such grand-scale behavioural patterns can only be fully understood and protected from global change if the complete behavioural cycle, as embedded into the periodic environment, is considered from an evolutionary and mechanistic perspective (Helm et al. 2013, Visser 2010, Wilcove and Wikelski 2008). Life history theory (see Stearns 2004 for review) predicts that natural selection and other evolutionary forces led to the evolution of optimal behaviours that ensure highest fitness in terms of long-term reproductive success (McNamara et al. 2001) under the given ecological constraints.

In mathematical biology, game theoretic approaches help to understand complex decision-making processes that lead to the maximization of fitness and the evolution of optimal strategies (Houston et al. 1988, McNamara et al. 2001, Parker and Smith 1990). Notably, stochastic dynamic programming (SDP) can be applied, which is a well-known method for solving multi-stage decision problems (Bertsekas 2005, Parker and Smith 1990). In periodic environments, we face the additional problem that behavioural cycles need to be closed (Clark and Mangel 2000, Hostetler et al. 2015, Houston and McNamara 1999). To this end, the optimal annual routine (OAR) modelling framework has been introduced (Houston and McNamara 1999, McNamara et al. 1998). Grounded in state-based life history theory, it assumes that evolution shapes the behaviour of animals by natural selection and that an animal takes its behavioural decisions based on knowledge

of its environment as well as its own state. These assumptions allow for an optimization-based approach like SDP to identify state-dependent optimal life-history strategies of organisms under cyclic environmental conditions (McNamara and Houston 2008).

Although the OAR framework is suited for a broad range of research questions and has many advantages over other modelling approaches, the number of actual implementations is small (Feró et al. 2008). One major reason for this might be the complexity of such models, which require time and expertise for model development and implementation. Here, we present the software package sOAR that provides an open source implementation of the original OAR framework by Houston and McNamara (1999). We further extended the framework by certain optional features that are crucial for studying bird migration and account for flight ability and wind-dependent migration costs. sOAR provides a computationally fast and ready-to-use OAR software, which is implemented in a modular manner in C++ allowing easy adjustment for specific research questions.

Theoretical Background

The key ingredients of stochastic dynamic programming (SDP) are state variables, decisions and a currency to evaluate decisions. The set of possible decisions, or available behavioural activities, at time t depends on the state X_t of the animal. The main objective is finding the optimal strategy that maximises pay-off, for example the long-term reproductive success (Houston and McNamara 1999, Mangel 2015). The optimal strategy takes the short- and long-term costs and benefits of any particular decision into account, as well as the associated probability of surviving the activity and the probability that the animal's state is changed by a certain increment when the activity is performed (Mangel

2015). The decision costs can depend on internal (e.g. metabolism) but also on external constraints (e.g. food availability) (Bauer and Klaassen 2013).

The development of state X_t of an organism at time t under the given constraints, costs and benefits is modelled as a discrete-time dynamical system with usually nonlinear difference equations of the form

$$X_{t+1} = F(X_t, A_t, W_t), \quad t = 0,1, \dots, T-1 \; with \, X_0 = const., \qquad (1)$$

where A_t is the vector of decision variables to be selected in the process, W_t is a random parameter with given probability distribution, T represents the time horizon, X_0 is the initial state and F is a function specifying the system's transitions in state with time. In general, though the concrete result of a given action will be unknown, the probability distribution of states X_{t+1} resulting from state X_t and action A_t taken at time t can be estimated (Bertsekas 2005).

Subject to this random sequence of constraints (eq. 1), a planned sequence $\{A_t^*\}_{t=0}^T$ of behavioural decisions conditional on the sequence of realized states shall be selected that maximizes the payoff. By Bellman's Principle of Optimality (Bellman 1957) and the law of iterated expectations, the maximum payoff $V(X_t)$ to be expected given state $\mathrm{X_t}$ is

$$V(X_t) = \max_{A_t}\{U(X_t, A_t) + \lambda \mathbb{E}[V(X_{t+1})]\}, \qquad (2)$$

where $\mathrm{U}(X_t, A_t)$ is the utility or immediate reward of being in state X_t performing action A_t and $\mathbb{E}[V(X_{t+1})]$ represents the expected value of being in state X_{t+1} at the next time step. The discounting factor λ equals one when a population is following an assumed evolutionary stable strategy. Thus, if the optimal payoff at final time T is given ($V(X_{t+1}) = V(X_T)$), the expected maximum payoff can be calculated recursively for each combination of state and time by using the appropriate transition probabilities between states X_t and

X_{t+1} (eq. 1) and maximizing only the immediate utility $U(X_t, A_t)$ in each case at a time. Simultaneously, the optimal sequence $\{A_t^*\}_{t=0}^T$ of decisions for all potential sequences of states that could realize is obtained, i.e. the optimal strategy.

For computational reasons, the optimal strategy is usually computed by backward induction, starting from the known (or desired) end state and moving backwards in time until convergence. Hereby, suboptimal solutions are omitted during the search as illustrated in Houston et al. (1988). In the context of optimal annual routine modelling, the terminal reward $V(X_T)$ is assumed to equal one for all possible states. Further, consecutive periodic time cycles are connected by setting the state and payoff at the end of one cycle equal to the state and payoff at the beginning of the next cycle (Houston and McNamara 1999). Iterating over successive time cycles to convergence may then result in the best strategy maximizing the expected number of descendants left in the distant future. Once the optimal strategy has been computed, it can be applied in simulations of population dynamics or individual life histories under the optimal strategy, e.g. for predictive modelling.

Model description

The model considers the behaviour of a female animal and its female descendants over a specified number of periodically reoccurring stages or decision epochs respectively. For example, the animal has to make behavioural decision at each week of an annual cycle. The animal itself is described by the state variables energy reserves, health condition (optional), age of offspring, experience, location, and migratory state (optional). Their uniform discretization is user-defined, whereby the location variable is currently implemented for up to two different sites. An overview of the implemented state variables is provided in Table 1 (for details see Supplementary material Appendix 1, Table A1).

At the beginning of each stage the animal selects a behavioural action (cf. Table 1). For an animal without dependent offspring these are either initiating reproduction, subsisting or migrating (optional). Potential activities of an animal with dependent offspring are caring for the offspring or abandoning it. Simultaneously, the animal must choose a foraging intensity at each decision epoch, ranging from zero (no feeding) to one (maximum possible energetic intake of available resources). If an animal with dependent offspring cannot forage with sufficient intensity to balance the offspring's energy needs, this is abandoned.

Each behavioural action is associated with the following costs that influence the animal's future state (Supplementary material Appendix 1, Table A1): metabolic energy costs that increase with foraging intensity, and additional energetic costs for reproduction and migration. If health condition is included in the model, it will also be affected by costs for metabolism, reproduction and migration. Further, there are expected energetic gains from foraging that increase with foraging intensity, food availability and experience. Energy intake is coupled to experience assuming that young animals may have a lower foraging efficiency than adults. The coupling happens via a parameter θ with $0 < \theta \leq 1$, which scales the actual energy intake of an animal with low experience *s*uch that it will be a certain fraction of the intake of an animal with full experience. The parameter θ implicitly accounts for density dependence and is usually adjusted during computations until the population growth rate equals 1, meaning the population is in a stationary state with constant population size (see Houston and McNamara 1999, Supplementary material Appendix 3).

The animal faces different sources of mortality: starvation, predation and disease (optional). Starvation and disease correspond to reserves and health condition dropping to their minimum level. The user-defined predation rate can increase with foraging

intensity and higher levels of reserves. It is specified for each location and the migration period, respectively, and may include a background mortality. Disease risk rises with decreasing values of the health variable. If this variable is enabled, a background mortality for disease is determined in sOAR that reflects the maximum life expectancy of the species. If a parent animal dies, its dependent offspring dies, too.

sOAR can be run as a pure reproduction model or can optionally include migration between two locations. In both models, environmental food availability is specified by a periodic function of time and location. Migratory costs can be time and reserves dependent but since migrating model animals cannot forage, these user-defined costs need to integrate potential energy gains through foraging for species that in reality feed during migration. We introduced an option to read in periodic migratory costs from file, which can mirror cyclic wind conditions like thermals that allow energy-efficient soaring flight of avian migrants. However, in principle this option allows time-dependent migration costs for any animal. Additionally, the respective share of active (flapping) and passive (soaring/gliding) flight regarding total flight costs is determinable. Migration may span several decision epochs but must be completed without pause once started. During that time, the state variable indicating the state of migration increases while the location variable indicates the place of origin until the last week of migration upon which the animal will be relocated and the migratory state be reset.

To determine the optimal strategy, behavioural actions are evaluated in terms of their associated long-term reproductive success. Subsequently, the computed optimal strategy can be employed in Markov chain iterations (forward iteration). The values of the resulting steady state distribution represent the probability of an individual or the proportion of a population that follows the optimal strategy to be expected in any particular state-time combination. Thus, population dynamics under the optimal strategy

emerge from the simulation allowing to analyse behavioural timing, proportions of a population performing a behaviour, age structures, mortality patterns and the development of mean reserves and health condition.

A detailed model description and instructions on running sOAR are provided in the User Manual (Supplementary material Appendix 3). Figure 1 illustrates the workflow of sOAR including required inputs and produced output files, while Figure 2 provides a model overview.

Illustrative examples

We illustrate sOAR by simulating the effect of seasonality in the wintering habitat on the timing of migration and reproduction in a migratory bird. Using a hypothetical migratory bird we show sOAR's capability to determine a complete life-history strategy based on differing cyclic environmental conditions at two distinct locations representing the breeding and wintering habitat. Ecologically, the example reveals how the degree of seasonality in the wintering habitat may alter the optimal timing of migration and reproduction. Moreover, it shows that the optimal timing of behaviour depends on the state of the animal and that different degrees of synchrony between adult and juvenile behaviour might arise from different environmental conditions.

In the example, both the health variable and the migration option were enabled. Biological parameter settings (Supplementary material Appendix 2, Table A2) were oriented at a medium-sized long-distant migrant as from the genus *Falco*, employing active flapping flight. The two locations can be interpreted as a temperate and a more tropical location in the same hemisphere, meaning that seasonal food availability (following a sine curve) was synchronised but the tropical location showed much lower seasonality despite the same yearly average. We computed the optimal behavioural strategy for three scenarios with

different degrees of seasonality in the wintering habitat such that the maximum potential energy gain from foraging in the two locations differed by approximately 25 % (subtropics), 30 % and 35 % (high tropics) during peak times (Supplementary material Appendix 2, Figure A1). Sample scripts and detailed instructions are provided in the supporting information.

The preferential departure date of autumn migration varied depending on seasonality of food supply in the wintering habitat whereas the onset of spring migration and breeding was very similar across scenarios. For lower degrees of seasonality in the wintering location (high tropics compared to more seasonal subtropics), the timing of autumn migration varied considerably between experience classes (Figure 3a-c), and depending on the level of reserves (Figure 3d-f) and health condition (not shown). Timing of spring migration was overall less variable because the optimal timing of spring migration is more influenced by conditions in the breeding habitat and because only mature birds return to summer grounds to attempt breeding, as emerging during the solution of the model. At the same time, the time window of spring migration was longer when overwintering in more seasonal subtropics because building up reserves after strenuous autumn migration was less effective than in tropics because of the more pronounced resource low during winter. Hence, overall, differences in seasonal food availability between different locations may induce large variances in migration patterns. No major differences in the optimal timing of the breeding period occurred but the highest food abundance coincided with the hatching of the young for all settings.

We note that time slots of favourable wind conditions might be similarly important in driving the timing of migration in soaring and gliding birds since passive flight can decrease their energy consumption during migration considerably (Pennycuick 1972), which can be further explored using sOAR.

238 A second example illustrates how the optimal number of brood cycles per year of non-
239 migratory birds decreases with increasing fledging age of the offspring (Figure 4,
240 parameters settings and configuration file in Supplementary material Appendix 2, Table
241 A3, and Supplementary material Appendix 5). Here, the migration option and the state
242 variable of health condition were not included in the model. The sOAR software has
243 further been tested on the optimal annual routine models of Houston and McNamara
244 (1999) and a migration model oriented at McNamara et al. (1998). The results were
245 consistent with those published except for minor differences which we attribute to
246 potential differences in the actual implementation of the model and in selected model
247 settings regarding e.g. the convergence criterion and stochasticity settings for energy
248 reserves and health condition. The respective configuration files and some visual results
249 can be found in the sOAR User Manual (Supplementary material Appendix 3).

250 Conclusion

251 sOAR provides a powerful and user-friendly implementation of the optimal annual
252 routine framework by Houston and McNamara (1999) for computing optimal life history
253 strategies of animals under periodic environmental conditions and simulating their
254 population dynamics given such a strategy. Facilitating theoretical studies of animal
255 behaviour, it will improve our understanding of how natural selection shapes trade-offs
256 in animal behaviour within cyclic environments. We further extended the original
257 framework to differentiate between the costs of active and passive flight and to consider
258 periodic wind conditions acting on birds during migration. This will allow studying the
259 timing of migration between obligate soaring vs. flapping birds, or studying ontogenetic
260 differences in birds where soaring vs. flapping flight is age dependent (Hake et al. 2003).

Our main illustrative example showed how the optimal timing of spring and autumn migration may vary with environmental food supply at a site. Such insights are particularly interesting in the face of global change that may differently alter food availability in different regions. Changing environments may render current behavioural strategies of migrants and other animals suboptimal with potentially negative effects on population dynamics such that, in the long-term, a new optimal strategy should be adapted in order for a population to persist. Such facets, the consequences of suboptimal behaviour or the development of new behavioural strategies, can be easily explored using sOAR. Also, individual variation can be explored within OAR frameworks and be compared to empirically observed movement data, for example by means of telemetry (Feró et al. 2008). To illustrate usage and ease application, the software package sOAR includes descriptions and configurations for two illustrative examples as well as two examples from the literature (Figures 3-4 and Supplementary material Appendix 3).

The following list provides a summary of potential applications of sOAR (cf. Feró et al. 2008) whereby additional sites and processes such as molt or explicit density-dependent effects (Barta et al. 2008) or thermoregulation could be integrated into future versions of sOAR:

- Analysis of life-history constraints under global change
- Prediction of potential new adaptive behavioural strategies
- Theoretical studies of carry-over effects at the population level
- Analysis of phenotypic variation in a population within a life-history context
- Studies of functional groups of organisms
- Combining life-history models with large-scale datasets that are becoming increasingly available nowadays

Overall, such analyses will contribute to better understanding the different constraints on movement and behaviour of individuals and the consequences for population and community dynamics (Jeltsch et al. 2013, Nathan et al. 2008).

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Data Accessibility

The sOAR application as ready-to-use binary distribution and as source distribution, with detailed manual, the configuration file used in this paper and sample R and Matlab scripts for processing the output, is accessible at https://sourceforge.net/projects/soar-animal-behaviour.

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Supplementary material (Appendix EXXXXX at <www.oikosoffice.lu.se/appendix>).
Appendix 1–6.

Figures

Figure 1. sOAR flow of use. User-defined settings provided by an input file are illustrated in the blue box, while the green boxes give an overview of the output files generated by the internal backward and forward iteration of sOAR (orange box).

Figure 2. Model overview for sOAR depicting the implemented interdependencies (arrows) between state variables (orange stars), behavioural activities (blue boxes), user-defined input parameters (grey ellipses), internal submodels (yellow ellipses) and sources of mortality (white boxes).

Figure 3. The timing of behaviour with respect to different experience (a–c, left) and reserve classes (d– f, right) for different degrees of seasonality in wintering grounds, ranging from very low seasonality of high tropics (top) to intermediate seasonality of subtropics (bottom), whereas seasonality of breeding grounds was very high as in temperate zones. Graphs represent the proportion of a population following the optimal strategy that performs a certain behaviour or has a certain condition over the year. Left: The timing of migration (blue), especially autumn migration, varies with seasonality in the wintering habitat, in contrast to the breeding period (black). Varying seasonality can induce synchronic or differential migration between individuals with low (dashed), medium (dotted) or high (solid) experience. Please note that only individuals of the highest experience return from wintering location in spring and attempt breeding. Right: The level of reserves on the onset of migration is depicted from high to low in pink, blue, yellow and green. Regardless of other factors, an early departure is optimal when reserves are high.

Figure 4. The optimal timing of initiation of breeding activities when the offspring becomes independent from the parent bird at the age of 3 (solid yellow), 4 (dotted blue) or 5 (dashed pink) weeks. Other model parameters than age of independence were kept constant. With increasing age of independence the optimal number of brood cycles decreases.

399 # Tables

400 Table 1. Overview of state variables and behavioural actions implemented in sOAR, and of user-defined costs, constraints and

401 response functions. Italic entries indicate optional settings.

State Variables:	Energy reserves, *health condition*, experience, age of offspring, location, *migratory state*
Actions:	Forage, start reproduction, care for offspring, subsist, *migrate*
Fixed costs and constraints:	Reproduction costs and constraints, growth and role of experience, maximum lifespan, basal metabolic rate, food availability, grade of stochasticity*, wind conditions*, *migration costs and constraints*
Response functions:	Metabolism, predation, *immune response, flight energetics*

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Appendix 1

Table A1. Overview of stage and state variables in sOAR, including a characterization of variables and their allowed range of values. The grid of each discretized variable is equally spaced. For energy reserves and health condition non-integer values are possible.

Variable	Characterization	Range of values
Time, t	Stage variable/decision epoch: at each stage of time a behavioural decision must be made.	$t \in \{0,1, \dots t_{max}\}$
Energy reserves, x	State variable: level of energy reserves within defined range.	$x \in \{x_{min}, \dots, x_{max}\}$ with $0 \leq x_{min} < x_{max}$ and $x_i - x_{i-1} = const.$
Health condition, y	Optional state variable: state of the immune system.	$y \in \{y_{min}, \dots, y_{max}\}$ with $0 \leq y_{min} < y_{max}$ and $y_i - y_{i-1} = const.$
Age of offspring, a	State variable: existence and age of dependent offspring. A value of -1 indicates no offspring, a value of 0 newly born offspring and values >0 the age of dependent offspring in number of decision epochs. Offspring becomes independent at a_{max}.	$a \in \{-1,0,1, \dots, a_{max}\}$
Experience, e	State variable: foraging experience of individuals, e.g. newly independent young might be less efficient at finding resources.	$e \in \{0,1, \dots, e_{max}\}$
Location, o	State variable: location of the animal. When migration is enabled, o can take one of two values representing the two locations between which the animal can migrate.	$o = 1$ or $o \in \{1,2\}$
Migratory state, s	Optional state variable: indicating if and how long the animal has been migrating; the total duration of migration (in number of decision epochs) is user-defined.	$s = -1$ or $s \in \{-1, 0, \dots, s_{max}\}$

Appendix 2

Table A2. Model parameters and their corresponding values or formulas as used in the example illustrating how the optimal timing of spring and autumn migration may vary with environmental food availability at a site. Where three values are given, these refer to the three simulated environmental scenarios. Extra costs of reproductive or migratory activities add to the cost of subsistence (details in the User Manual in Supplementary material Appendix 3).

Parameter	Symbol	Value / Formula
State and stage variables:		
Range of energy reserves	x	$\in [0,10], \in \mathbb{N}$
Range of health condition	y	$\in [0,10], \in \mathbb{N}$
Range of experience	e	$\in [0,2], \in \mathbb{N}$
Age of any offspring	a	$\in [-1, a_{incub} + a_{indep} + 2], \in \mathbb{Z}$
Location	o	$\in [1, n_{loc}], \in \mathbb{N}$
State of migration	s	$\in [-1, s_{migr} - 1], \in \mathbb{Z}$
Week of year	t	$\in [0,51], \in \mathbb{N}$
General biology:		
Background mortality by disease	M_{bg}	0.0016
Basic metabolic cost	c_b	2.0
Foraging intensity	u	$\in [0,1]$
Energetic cost of subsistence	$c_{subsist}$	$c_b*(1+0.01*(x/10)^2)+6u^2*(1+0.01*(x/10)^2)$
Health cost of subsistence	$h_{subsist}$	$1 - 0.2*c_{subsist} - 0.01*c_{subsist}^2$
Environment:		
Number of locations	n_{loc}	2
Average food availability at site 1	$A_{food}(1)$	1.0
Average food availability at site 2	$A_{food}(2)$	1.0
Degree of seasonality of food at site 1	$\varepsilon(1)$	0.1, 0.2, 0.3
Degree of seasonality of food at site 2	$\varepsilon(2)$	0.7
Predation risk at location 1 and 2	M_{loc1}, M_{loc2}	$0.01*u^2*(1+0.01*(x/10)^2)$
Probability of active flight	p_{act}	1.0

Reproduction:		
Duration of incubation in weeks	a_{incub}	4
	(= a_{max}-a_{indep}-2)	
Age of independence in weeks	a_{indep}	6
	(= a_{max}-a_{incub}-2)	
Energetic cost of starting a brood	c_{start}	0.5
Energetic cost of incubation	c_{incub}	1.5
Energetic cost of brood care	c_{care}	7.0
Health cost of starting a brood	h_{start}	1.0
Number of offspring	n_{brood}	2
Fitness of offspring at independence	f_{indep}	0.5
Computed equilibrium value for foraging efficiency of inexperienced bird (e=0)	θ	0.7165, 0.7581, 0.8123
Probability of increasing experience	p_{exp}	0.02
Migration:		
Duration of migration in weeks	s_{migr}	3
	= s_{max}+1	
Energetic cost of active flight	c_{act}	2.0
Reserves change during migration	Dx_{migr}	$p_{act}*c_{act}*(1+0.001*x^2)$
Health cost of active flight	h_{act}	1.0
Health change during migration	Dy_{migr}	$p_{act}*h_{act}$
Predation risk during migration	M_{migr}	$0.01*(1+0.01*(x/10)^2)$

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Table A3. Model parameters and their corresponding values or formulas as used in the simple example demonstrating that the optimal number of brood cycles per year depends on the age at which the offspring becomes independent from the parent. Where three values are given, these refer to the three varied values of the age of independency. Extra costs of reproductive activities add to the cost of subsistence (details in the User Manual in Supplementary material Appendix A3).

Parameter	**Symbol**	**Value / Formula**
State and stage variables:		
Range of energy reserves	x	$\in [0,10], \in \mathbb{N}$
Range of health condition	y	$\in [0,10], \in \mathbb{N}$
Range of experience	e	$\in [0,2], \in \mathbb{N}$
Age of any offspring	a	$\in [-1, a_{incub} + a_{indep} + 2], \in \mathbb{Z}$
Location	o	$\in [1, n_{loc}], \in \mathbb{N}$
State of migration	s	$\in [-1, -1], \in \mathbb{Z}$
Week of year	t	$\in [0,51], \in \mathbb{N}$
General biology:		
Basic metabolic cost	c_b	1.87
Foraging intensity	u	$\in [0,1]$
Energetic cost of subsistence	$c_{subsist}$	$c_b+(2u+3u^2)$
Environment:		
Number of locations	n_{loc}	1
Average food availability at site 1	$A_{food}(1)$	1.1
Degree of seasonality of food at site	$\varepsilon(1)$	0.2
Predation risk at location	M_{loc1}	$0.0019+0.004u^2$
Reproduction:		
Duration of incubation in weeks	a_{incub} (= a_{max}-a_{indep}-2)	2
Age of independence in weeks	a_{indep} (= a_{max}-a_{incub}-2)	3, 4, 5
Energetic cost of starting a brood	c_{start}	0.5
Energetic cost of incubation	c_{incub}	2.3

Energetic cost of brood care	c_{care}	4.6
Number of offspring	n_{brood}	1
Fitness of offspring at independence	f_{indep}	0.5
Computed equilibrium value for foraging efficiency of inexperienced bird (e=0)	θ	0.4998, 0.5133, 0.5260
Probability of increasing experience	p_{exp}	0.04

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Figure A1. Environmental food availability in the breeding (black) and wintering (red) habitat varying sinusoidal over the year. Average yearly food supply in both locations is the same but the degree of seasonality in the wintering habitat varies from low (solid, high tropics) to high (dashed, subtropics). Please note that the actual energetic gain of an animal further depends on foraging intensity and experience and is scaled according to the maximum possible energy level.