**Emergent coordination in a complex avian incubation system**

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**ABSTRACT**

**INTRODUCTION**

**METHODS**

**Model Descriptions**

*Basic Behavior: NULL model*

The NULL model describes the basic energetic of a breeding pair of adult Leach’s Storm-petrels and their single egg over an incubation season. See Table 2 for all parameter values and sources.

Each parent begins the incubation with an identical, deterministic initial energy value. For each discrete timestep (representing a 24-hour period), adult parents can be in one of two states: *incubating* or *foraging*. The only sex-specific difference in this model is that the female begins the season with the initial energy value in the *incubating* state, while the male begins the season with the initial energy value in the *foraging* state.

In the *incubating* state, the parent loses a deterministic amount of energy to incubation metabolism. After suffering the metabolic cost, the parent will deterministically switch to the *foraging* state if its energy level has fallen below a threshold (TODO REMOVE <= -> < IN MODEL).

In the *foraging* state, the parent loses a deterministic amount of energy to foraging metabolism, but also stochastically gains energy. This stochastic foraging energy intake is randomly drawn from a normal distribution with an empirically-derived mean and standard deviation (TODO REMOVE CONCATENATION FROM MODEL). After both metabolism and energy intake, the parent will deterministically switch to *incubation* state if its energy level has passed above a threshold.

(TODO SWITCH EGG BEHAVIOR TO BEFORE PARENT BEHAVIOR ALL MODELS)

Before any parent behavior occurs for the timestep, the egg is either incubated (if one or both parents are in the *incubating* state) or neglected (if neither parent is in the *incubating* state). For each day being incubated, the egg moves one timestep closer to its hatch date. On the other hand, for each day of neglect, the egg not only does not move closer to the hatch date, but also pushes the hatch date further due to the developmental cost of being left cold (Boersma and Wheelwright 1979). Thus, there are two ways for the season to end: the egg successfully hatching after being sufficiently incubated over the course of the season, or the season hitting a maximum timestep limit wherein the hatch date has been continually pushed later due to repeated neglect. In the latter case, the egg never hatches, and the season is recorded as a failure. (TODO ADD NEGLECT STREAK FAILURE?).

*Simple coordination: OVERLAP models*

The OVERLAP\_SWAP model inherits the entirety of the NULL model, with a single additional rule that represents a simple coordination behavior. After parent behavior each day (including switching states following the NULL energetic threshold rules), this model then determines if both parents are in the *incubating* state. If both parents are *incubating*, the parent that was *incubating* the previous timestep is automatically switched to the *foraging* state before the beginning of the next timestep. Thus, in this model, only one parent incubates at a time, and the arrival of a parent to the nest after foraging will automatically trigger the departure of an already-incubating mate, even if that mate’s energy level has not yet fallen below the standard energetic threshold.

The OVERLAP\_RAND model tests a slight alteration of the OVERLAP\_SWAP model. In this model, if both parents are *incubating* at the end of the timestep, then with *equal, random chance* a single parent is switched to the *foraging* state before the beginning of the next timestep, independent of either the standard energetic thresholds or which parent was previously incubating.

*Sex-specific costs: SEXDIFF model*

The SEXDIFF model inherits the entirety of the OVERLAP\_SWAP model, with a single additional rule that represents the energetic cost of egg production to the female. Before the first timestep of the breeding season, the female parent’s initial energy value is multiplied by a coefficient ranging from 0.0 to 0.9 (tested for each 0.1 increment). The male’s energy profile is unaltered. This cost is a conservative estimate of the energetic cost in a species whose egg can equal up to 25% of the mass of the breeding female (

*Sex-specific compensation: SEXCOMP models*

*Environmental shifts: FORAGINGDIFF models*

**Implementation and Analysis**

All of our models were implemented using an object-oriented approach in C++, which was compiled and run directly through R using *Rcpp* (Eddelbuettel et al. 2011). Each model (or parameter set for a given model) was run for 100,000 independent iterations that shared a single, uniquely seeded pseudorandom number generator. All models were monitored for a suite of output variables including hatch success, overall incubation length, the final, mean, and variance energy values of each parent across the incubation season, as well as the length and number of their *foraging* and *incubating* bouts. Output analysis and visualization was conducted in R using *tidyverse* packages (Wickham 2017). A repository containing all model, analysis, and visualization code is available at <https://github.com/ltaylor2/LHSP>.

**RESULTS**

*Basic behavior*

*Simple coordination*

*Sex-specific costs*

*Sex-specific compensation*

*Environmental shifts*

**DISCUSSION**

**ACKNOWLEDGMENTS**

**LITERATURE CITED**

**FIGURES AND TABLES**

**Table 1.** Concise descriptions for the models applied to investigate Leach’s Storm-petrel incubation behavior. All models include adult storm-petrel parents—one of each sex—and a single egg.

|  |  |
| --- | --- |
| **Model name** | **Description** |
| NULL |  |
| OVERLAP\_SWAP |  |
| OVERLAP\_RAND |  |
| SEXDIFF |  |
| SEXCOMP\_OVERLAP |  |
| SEXCOMP\_THRESH |  |
| FORAGINGDIFF\_VAR |  |
| FORAGINGDIFF\_MEAN |  |

**Table 2.** Energetic and behavioral parameters of Leach’s Storm-petrel adults and eggs for all models. As described in the main text, some models include coefficients to adjust these parameters.

|  |  |  |
| --- | --- | --- |
| Parameter | Source | Note |
|  |  |  |
|  |  | Includes distributed cost of flying to and from foraging grounds |
|  |  |  |
|  |  |  |
|  |  |  |
|  |  |  |
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