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## **TernCOLONY 1.0 Model Description**

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## Abstract

TernCOLONY is an individual-based model of Least Tern reproduction. The model simulates the reproduction of all individuals within virtual Least Tern breeding populations on large rivers below multi-purpose dams. Breeding seasons are simulated in daily time steps. Users may specify different habitat inputs, representing excellent and degraded nesting habitat conditions. After choosing baseline habitat conditions for simulations, users may choose to add “restoration” sandbars to simulations to understand how different scenarios of habitat creation may affect regional reproduction. In addition to specifying habitat conditions, users may specify a range of daily flow inputs (simulating reservoir operations during wet years, dry years, or years with mid-season floods). Users may also specify a range of predator and human disturbance intensities or initial tern population sizes. By repetitively simulating different scenarios of initial conditions, users may learn if and how different factors limit regional Least Tern reproduction or how alternative management strategies may perform to increase reproduction. This document, the model description, is the first in a series of publications that describe the TernCOLONY model. The TernCOLONY model description follows the “ODD” (Objectives, Design Concepts, and Details) protocol of Grimm et al. (2006) as updated by Grimm et al. (2010) for describing individual-based models. This protocol starts with general and conceptual characteristics (sections 2-5); followed by the detail needed to make the model reproducible (sections 6-8). Full context for the model development, testing, and analysis process is given in Lott et al. (2012a), which also contains sections describing major model inputs (e.g., habitat and flow datasets) for specific study sites. Most users will access TernCOLONY via the web-based graphical user interface located at <http://www.leasttern.org>. The model description provides the foundation upon which all subsequent publications related to TernCOLONY will rely.

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# Contents

<b>Abstract</b> .....	<b>ii</b>
<b>Figures and Tables</b> .....	<b>v</b>
<b>Preface</b> .....	<b>vi</b>
<b>Unit Conversion Factors</b> .....	<b>viii</b>
<b>1 Introduction and Objectives</b> .....	<b>1</b>
1.1 Document objectives.....	1
1.2 Document conventions.....	1
1.3 Units and modeling conventions.....	2
<b>2 Model Purpose</b> .....	<b>3</b>
<b>3 State Variables and Scales</b> .....	<b>4</b>
3.1 Management areas.....	4
3.2 Sites.....	5
3.3 Cells.....	7
3.4 Adult terns.....	8
3.5 Nests.....	9
3.6 Chicks.....	9
3.7 Mortality agents.....	10
<b>4 Process Overview and Scheduling</b> .....	<b>11</b>
4.1 Habitat update.....	11
4.2 Adult arrival.....	11
4.3 Adult colony site selection.....	12
4.4 Adult mating.....	12
4.5 Nest initiation.....	12
4.6 Egg laying.....	13
4.7 Hatching.....	13
4.8 Chick fledging.....	14
4.9 Mortality.....	15
4.9.1 <i>Flooding mortality of nests</i> .....	16
4.9.2 <i>Flooding mortality of chicks</i> .....	16
4.9.3 <i>Predation and disturbance mortality</i> .....	16
4.9.4 <i>Mortality due to the death of both parents</i> .....	16
4.9.5 <i>Mortality due to parental abandonment</i> .....	16
4.10 Site abandonment by adults.....	17
4.11 Re-nesting.....	17
4.12 Reproductive failure.....	18
4.13 Output.....	19

<b>5</b>	<b>Design Concepts .....</b>	<b>20</b>
5.1	Emergence.....	20
5.2	Adaptation.....	20
5.3	Objectives, learning, prediction .....	21
5.4	Sensing .....	21
5.5	Interaction.....	21
5.6	Stochasticity.....	22
5.7	Collectives .....	22
5.8	Observation.....	22
<b>6</b>	<b>Initialization .....</b>	<b>24</b>
6.1	Habitat initialization .....	24
6.2	Adult tern initialization .....	25
<b>7</b>	<b>Time-Series Input Data: Daily Flows.....</b>	<b>26</b>
<b>8</b>	<b>Submodel Details .....</b>	<b>28</b>
8.1	Habitat update submodel .....	28
8.2	Adult initialization submodel.....	31
8.2.1	Arrival dates .....	31
8.2.2	State variable initialization .....	35
8.3	Adult clutch size submodel .....	38
8.4	Adult site identification submodel .....	38
8.5	Adult colony site selection submodel .....	40
8.6	Adult mating submodel .....	40
8.7	Nest readiness submodel .....	41
8.8	Nest site selection submodel.....	41
8.9	Egg laying submodel.....	42
8.10	Predation and disturbance mortality submodel .....	42
8.11	Site abandonment submodel .....	46
8.12	Random number generation.....	49
	<b>References.....</b>	<b>50</b>
	<b>Appendix A: Standard Parameter Values .....</b>	<b>52</b>
	<b>Appendix B: Example Mortality Agent Input .....</b>	<b>54</b>
	<b>Appendix C: Output Summary Statistics.....</b>	<b>56</b>
	<b>Report Documentation Page</b>	

# Figures and Tables

## Figures

Figure 1. Habitat quality functions.....	30
Figure 2. Distributions of nest initiation dates observed on the Missouri River, 2000–2006 data.....	34
Figure 3. Five replicate simulations of adult tern arrival dates, differing only in the random Poisson distribution draws. ....	36
Figure 4. Frequency histograms illustrating the effects of nest predators on model tern colonies across 1000 simulated breeding seasons.....	44

## Tables

Table 1. GUI-observable events. ....	15
Table 2. Nesting habitat quality parameters. ....	30
Table 3. Missouri Basin nest initiation data relevant to arrival parameter estimation.....	35
Table 4. Example previous-year location input (from the Keystone Reach, Arkansas River). ....	37

## Preface

The TernCOLONY simulation model is an individual-based model of Least Tern reproduction that was developed to better understand how reservoir operations (and other management activities) affect Least Tern breeding populations on large rivers. The model was collaboratively developed by American Bird Conservancy (ABC) and Lang, Railsback, and Associates (LRA). Colin Sheppard developed the model software and database. Dr. Richard Fischer of the U.S. Army Engineer Research and Development Center (ERDC), Environmental Laboratory (EL), provided feedback throughout model development. This effort was supported by funding from the U.S. Army Corps of Engineers Dredging Operations and Technical Support (DOTS) and the Dredging Operations and Environmental Research (DOER) programs.

This document is the first in a series of three documents related to the TernCOLONY model. The model has been extensively verified and rigorously tested using pattern-oriented modeling approaches (Grimm and Railsback 2005) and standard analytical techniques such as sensitivity analysis and parameter calibration. These tests and procedures are reported in Lott et al. (2012a). TernCOLONY is unique in that it is completely accessible via the web at <http://www.leasttern.org>. Lott et al. (2012b) provides a guide for preparing model inputs for those seeking to implement the TernCOLONY model in new locations. Additional documentation of the model's software and code is also available at <http://www.leasttern.org>.

The habitat and flow inputs underlying the first regional application of TernCOLONY (on the Arkansas River below Keystone Dam) were documented previously in Lott and Wiley (2012), which described research on Least Tern nesting habitat measurements that was funded by the U.S. Army Engineer District, Tulsa.

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<http://www.leasttern.org>.

During the preparation of this work, Antisa Webb was Chief of the Ecological Resources Branch; Dr. Edmond Russo was Chief, Ecosystem Evaluation and Engineering Division; The Program Manager for DOTS and DOER at the ERDC was Dr. Todd Bridges, Senior Research Scientist for Environmental Science. Dr. Elizabeth Fleming was Director, EL. The Commander of ERDC was COL Kevin J. Wilson. The Director of ERDC was Dr. Jeffery P. Holland.



## Unit Conversion Factors

Multiply	By	To Obtain
acres	4,046.873	square meters
cubic feet	0.02831685	cubic meters
feet	0.3048	meters
inches	0.0254	meters
miles (U.S. statute)	1,609.347	meters
miles per hour	0.44704	meters per second
square feet	0.09290304	square meters

# 1 Introduction and Objectives

## 1.1 Document objectives

This document describes an individual-based model (IBM) of Interior Least Tern (ILT) reproduction. The model simulates the arrival of adult ILT to breeding areas after spring migration; the selection of nest sites given variable habitat conditions; nest and chick mortality or survival; and re-nesting after nest or chick mortality. This biological model is nested within an analysis structure that allows users to simulate the response of tern populations to various types of management treatments under a wide range of habitat and initial conditions.

The model description follows the “ODD” (Objectives, Design Concepts, and Details) protocol of Grimm et al. (2006) as updated by Grimm et al. (2010) for describing IBMs. This protocol starts with general and conceptual characteristics (sections 2-5), followed by the detail needed to make the model reproducible (sections 6-8). Full context for the model development, testing, and analysis process is given in Lott et al. (2012a), which also contains sections describing major model inputs (e.g., habitat and flow datasets) for specific study sites.

The model is implemented in the *Repast Symphony* platform (<http://repast.sourceforge.net>), model inputs and outputs are managed in a *Postgres* relational database, and the model is run from a web-based graphical user interface (GUI) at <http://www.leasttern.org>.

This version of the model description, 1.0, is implemented in Version 3.4 of its *Repast Symphony* software, which uses version 10.2 of the *Postgres* database for input and output. Full documentation of the model’s software and code is available at <http://www.leasttern.org>.

## 1.2 Document conventions

The following conventions are used in this document to link the model description to the database and other project documentation.

- State variables that correspond to fields within tables of the *Postgres* relational database are italicized and labeled by their database field name (e.g., *celElev*).
- Database table names are listed in bold type surrounded by parentheses (e.g., “**(tblSite)**”).
- State variables not in the database are not italicized and have simple descriptive names in plain text (e.g., “list of the cells in the site”).
- Default model parameters (equation coefficients, etc. that normally do not vary among sites or model runs) are listed in bold and italicized type (e.g., ***nestIncubationDurationMean***). The basis for default parameter values is given in the model description and all model parameters, with their default values, are listed in Appendices A and B.
- Names of software platforms are italicized (e.g., *Postgres*).
- This document describes what types of inputs are needed (Sections 6 and 7), but inputs for specific model applications are documented in Lott et al. (2012b).

### 1.3 Units and modeling conventions

The following conventions are used throughout the model’s description and software. The authors use English measurement units, rather than metric, for the sake of familiarity to most potential users. The conventions apply to any variable unless an exception is specifically noted.

- Distance units are feet (ft) for variables at the site and smaller scales, and miles (mi) at larger scales.
- Area is in acres (ac).
- Elevations are in U.S. survey feet above sea level (e.g., 521.74 ft.) relative to the NGVD 1929 vertical datum, using a precision of 0.01 ft.
- River flows are in cubic feet per second (cfs).
- Spatial coordinates (e.g., data defining sandbar habitat) must be in standard xy coordinate systems, which may vary among model applications. For example, on the Arkansas River in Oklahoma, the authors used xy coordinates in the Oklahoma State Plane South coordinate system.
- Corps of Engineers River Miles (RM) are used for naming and spatial reference. RM represent benchmarks in historic river channels that have changed considerably. Thus, river miles are not used for measuring distances along recent channels.
- Time units are days (d).

## 2 Model Purpose

The purposes of this model are to:

- Increase understanding of what factors limit ILT reproduction (and how these vary in response to changes in habitat conditions);
- Compare the expected performance of alternative management strategies for increasing ILT reproductive success; and
- Inform decisions about river management (e.g., dam releases) or the direct management of threats to ILT populations (e.g., predator control).

The authors designed the model so that each of the four potential limiting factors listed below can be explored through model analysis:

- Amount and quality of sandbar nesting habitat
- Nest and chick mortality due to flooding from dam releases
- Predation on nests, chicks, and adults
- Nest and chick mortality due to off-road vehicles (ORVs)

Version 3.4 of the tern model is designed specifically for ILT nesting on river sandbars, where daily flow variation strongly affects habitat. This model could be applied to any river where the necessary habitat and flow input data are available (Lott and Wiley 2012). Least Terns also breed widely on coastal beaches (and on nearby rooftops). The model of reproduction described herein would work for any habitat type; however, using this model to represent breeding on coastal beaches or roofs would require modifications to how it represents habitat and how habitat affects adult tern colony and nest site selection.

### 3 State Variables and Scales

The model's spatial extent (the total distances represented) and resolution (site and cell sizes) are discussed below in the description of "Management areas," "Sites," and "Cells." Cells represent specific locations that an ILT can select to build a nest; sites are isolated groups of cells (i.e., sandbars); and management areas are a collection of sites influenced by the same hydrologic events. The model is two-dimensional, with elevations represented as a state variable of habitat cells.

The temporal resolution (time step) is one day. The temporal extent of a model run is a single breeding season, which can vary in starting and ending dates according to parameters for the start of adult tern arrival after spring migration (Section 8.2) and the last fledging date (Section 4.8). The model stops after simulating the last fledging event of the breeding season (Section 4.8).

The following sections describe the model's entities and the state variables that characterize them. The authors distinguish between constant state variables and those that are updated at each time step. The authors do not include state variables that are simply calculated from other state variables (e.g., the number of birds or nests in a site, which can be determined from the list of birds, each of which has a variable for their site). The authors also do not include variables that track when events occur (e.g., tern nests do not have a variable for the date of their creation); instead, such events are tracked as entries in a table (**tblEvent**) of the *Postgres* database.

#### 3.1 Management areas

A management area is a collection of sites that represents all of the potential nesting areas for one subpopulation of terns. Many different definitions of subpopulations are possible but the authors specifically defined a management area as a collection of sites that are all affected to some degree by the operations of a single large dam. Management areas have two purposes:

- Processes, parameters, and variables characterizing tern populations at an above-site level belong to management areas.

- Results are summarized and displayed by management area to understand dynamics at the defined subpopulation level.

Management areas are labeled by a management area code (*manCode*) and name (*manName*).

The primary state variable of a management area is its list of sites (Section 3.2); this list is created from a parameter (***manareaSiteCodes***) that specifies which sites are to be included in a particular model run.

A second group of state variables defines the river thalweg (the deepest part of the channel) within the management area as a set of points evenly spaced at 100 ft increments, from the dam to the downstream boundary of the management area. These thalweg points are used to locate objects in the upstream-downstream direction, e.g., in the site identification submodel (Section 8.4).

Thalweg points also define “reaches,” which are labels for sections of the management area’s river channel. For example, a new reach can start at each major tributary. Reaches are used only to label results.

The variables for each point on the thalweg are:

- Its coordinates *thwPointX* and *thwPointY* (for display convenience, point location is also provided as a GIS point geometry object);
- A reach name *thwReachID* (a character string); and
- The distance along the thalweg from the point to the upstream end of the management area, *thwMilesFromDatum*.

A third group of management area variables are the parameters that define the number and timing of adult tern arrivals (Section 8.2) and predator and ORV intensities (Section 3.7).

Dynamic characteristics of a management area (e.g., the number of adult terns; the number of fledglings) are simply calculated from the number of adults, nests, etc. at each of the area’s sites.

### 3.2 Sites

A “site” represents an isolated group of habitat cells where terns may nest. Version 3.4 has only two site types: river sandbars and constructed

sandbars. However, future versions could include other types, such as sand and gravel pits, salt flats, rooftops, reservoir islands, or coastal beaches. Sites comprise a collection of cells (Section 3.3) that represent habitat variables that vary over space within the site. The number, location, and characteristics of sites are determined from model input.

The following group of site variables defines static characteristics:

- *sitManAreaID* and *sitReachID*—The management area and reach that the site is in.
- *sitHabitatInputSet*—An identifier for the habitat input set being used. This identifier allows the input database to include several alternative sets of habitat input for the same management area (e.g., sandbars below Keystone Dam on the Arkansas River as measured in 2008 or in 2012). All the sites with the same value of *sitHabitatInputSet* belong to the same unique habitat input set.
- *sitSiteTypeID*—The type of site (e.g., natural sandbar, constructed sandbar).
- A list of the cells in the site.
- *sitCellLength*—The width (ft) of the site's square cells. The choice of cell size should consider topographic and habitat resolution (how steeply elevation changes, general size of vegetation patches, etc.), site size (small cell sizes could produce extremely high numbers of cells), and the methods and resolution of the data and analysis used to produce cell input. The standard value of this parameter is 6 ft, so each habitat cell represents 36 ft<sup>2</sup>.
- *sitMinSuitableFlow*— This variable represents frequently occurring flows (in cfs) that are likely to constrain Least Tern nesting during site selection. In management areas with hydropower production, this is typically the flow resulting from full hydropower production. Nests placed below the water surface elevation (WSE) at this flow are very likely to be inundated; nests above that WSE are likely inundated only due to runoff or reservoir spill events. In relatively short management areas, all sites may have the same value of this variable, but it can change with distance below the dam in longer areas.

A group of six variables, called *sitFlowToElevA* through *sitFlowToElevF*, store coefficients for site-specific log-quadratic models that are necessary to calculate WSE from peak daily flow inputs at each site (Section 8.1).

A second group of site variables (listed below) defines daily habitat conditions. These variables depend on the daily maximum WSE at the site, which is calculated from daily maximum flow.

- *ssmSuitableAcres* (acres)—The area of all “suitable” habitat, regardless of its “quality” (Section 8.1).
- *ssmHighestQuality*—The habitat quality index of the site’s highest-quality cell (Section 8.1).
- *ssmDisplayHighQualityAcres*, *ssmDisplayMediumQualityAcres*, and *ssmDisplayLowQualityAcres*—The site’s area (acres) in each of three ranges of cell habitat quality; these ranges are defined by parameters (Section 8.1).

A final group of variables is used only for display and interpretation of results:

- *sitNearestCorpsRM*—The closest Corps of Engineers river mile to the site. This display variable may be preferred by users familiar with local river miles.
- *sitMilesFromDatum*—The site’s distance (measured via the management area’s river thalweg coordinates) downstream from the dam at the head of its management area.
- *sitPointX* and *sitPointY*—Coordinates used to display a site as a single point.

### 3.3 Cells

A cell is a square patch of habitat within a site, used to represent spatial variation. Each cell has static state variables set when the model is initialized:

- *celSiteID*—The site in which the cell is located.
- *celPointX* and *celPointY*—Coordinates of the cell’s center.
- *celElev*—The cell’s average elevation.
- *celCFSAtPoint*—The lowest flow (cfs) at which the cell is inundated (calculated from site-specific equations for the relationship between elevation and flow).
- *celDist2ForestEdge*—Distance (ft) from the cell to the nearest large tree either inside or outside of the active river channel.
- *celDist2Bank*—Distance (ft) from the cell to the nearest point on the bank (defined as the active channel margin).



- *celDist2Veg*—Distance (ft) from the cell to the nearest patch of low vegetation on the sandbar. In cases where distance to vegetation was not measured because there was no vegetation within measuring distance, the value of *celDist2Veg* is set to the arbitrary large number +9999).
- *celVegetation*—A yes (1) or no (0) variable for whether or not vegetation is present in the cell.
- Cell freeboard above peak hydropower—The elevation difference between the cell and the WSE at the flow specified by site variable *sitMinSuitableFlow*.

Cells also have state variables that change with time:

- Cell freeboard—The elevation difference between the cell and the maximum daily WSE (positive if the cell is above the WSE).
- Cell quality—A habitat quality metric defined in Section 8.1.

### 3.4 Adult terns

Adult terns represent the birds that return from migration, select a nesting site, lay eggs in nests, and raise broods of chicks until fledging. Adult tern state variables are:

- *adtManAreaID* and *adtSiteID*—The management area and site currently occupied by the adult.
- *adtSex*—Sex, equal to male or female. Males are represented explicitly, even though they have few behaviors, since unmated female terns require an unmated male tern to produce a nest.
- *adtReproductiveStatus*—A discrete variable with one of the following values: “unmated” (without a mate), “mated” (a mate has been selected; for females, this also means that actual reproduction has not yet started), “laying” (for females during egg-laying), “incubating” (for females when all eggs are laid and incubating), “brood rearing” (for females tending chicks), “successful” (meaning that at least one of the adult’s chicks has fledged), and “failed” (when it is no longer possible to produce any fledglings).
- *adtMateID*—The adult’s mate, a tern of the opposite sex.
- Arrival location—The location (described as one of the management area’s thalweg points; Section 3.1) where the adult arrives from migration and starts looking for a nesting site.

Adult females have an additional set of state variables related to their nesting status.

- *adtNestID*—The nest a female is currently incubating.
- Maximum clutch size—The maximum number of eggs that will be laid in the current nest.
- *adtBreedingAttempt* —The number of nests created so far in the current year.

### 3.5 Nests

Nests are represented instead of individual eggs because eggs can be tracked as nest variables. Static variables of nests are:

- *nesManAreaID*, *nesSiteID*, *nesCellID*—The management area, site and cell that the nest is located in.
- *nesFemaleID*—The female that created the nest.
- Incubation duration—The number of days between when the last egg is laid and when they hatch.

Additionally, three variables track the state of the nest over time:

- *nesNumNonViableEggs*—The number of nonviable eggs in the nest.
- *nesNumViableEggs*—The number of eggs that are viable (fertilized and capable of hatching) in the nest.
- *nesNumHatchedEggs*—The number of eggs that have hatched from the nest.

### 3.6 Chicks

A chick is a tern that has hatched from its nest and can move around its site, but cannot yet fly or move away from its site. Chicks are tracked until they “fledge” (e.g., turn into birds that can fly). Fledglings are not included in the model. Rather, fledging is recorded as an event in the database. Chicks have the following state variables, which do not change after the chick is created:

- *chkManAreaID* and *chkSiteID*—The management area and site where the chick occurs. (The location of chicks, like adults, is tracked by site; they are not assumed to be confined to any particular cell.)
- *chkNestID*—The nest that the chick hatched from.

- *chkMotherID*—The parent female.
- The date on which the chick will fledge (if it survives).

### 3.7 Mortality agents

Mortality agents are model objects that represent predators or human disturbances that cause direct mortality to adult terns, nests, or chicks.

Mortality agents act at the site level. While all sites are subject to the same kinds of mortality agents, each individual mortality agent kills terns at only the site where it arrives. Four kinds of mortality agents are defined by input (Section 8.10).

Mortality agents have two state variables that are categories used only for analysis of results.

- *mamName* and *mamCode*—The name and code of the specific type of mortality agent (e.g., nest predator, chick predator, adult predator, or ORV).

Mortality agents also have a number of state variables that specify where and how long they act once they have discovered a site and the magnitude of mortality they cause to different tern objects while they are present.

- *morSiteID*—The site where the mortality agent is located.
- Duration of stay—The number of days the agent will be active at the site.
- Adult kill rate—The mean number of adult terns the agent will destroy per day.
- Nest kill rate—The mean number of nests the agent will destroy per day.
- Chick kill rate—The mean number of chicks the agent will destroy per day.

## 4 Process Overview and Scheduling

This section provides a schedule of the model's major actions: what entities do and the order in which the actions are performed during the daily simulations. This schedule is an overview of how the model operates. Simple actions are described in full, with more complex processes treated as submodels that are described in detail in Section 8.

Throughout the model's schedule, various kinds of events are logged to the *Postgres* database for observation and analysis. These event logging actions are not described in this section but instead are compiled at Section 5.8.

The following subsections describe the model's actions, in the order in which they are executed each day.

### 4.1 Habitat update

Habitat is updated first because other model actions depend on habitat conditions. Habitat update details are in Section 8.1. The habitat update includes these actions:

- The date is incremented by one day.
- The daily maximum flows for all sites are input (Section 7).
- The sites update their daily maximum WSE from the daily maximum flow.
- Cells of each site update their flow-dependent variables.
- Site habitat variables are updated.

### 4.2 Adult arrival

New adult tern objects are placed in the model, simulating the arrival of adults from their spring migration. The number of adults that arrive on the current day, for each management area, is already known from the adult initialization submodel (Section 8.2), which is executed during model initialization. After being inserted in this action, new adults *do not execute* any other actions, including colony site selection, on the same day; they start executing all adult actions only on the following day.

### 4.3 Adult colony site selection

Adults that were created via arrival on the previous day, and adults that are re-nesting (Section 4.11) execute this action. The adult site identification submodel (Section 8.4) identifies the list of alternative sites from which the adult will choose a nesting site, and also specifies what the adult does if no sites are available. Then the colony site selection submodel (Section 8.5) determines which of those sites the adult attempts to nest in.

Once an adult selects a site, it “moves there”: the tern sets its *adtSiteID* variable to the selected site and is added to the site’s list of unmated adults. The tern’s arrival location (Section 3.4) is also updated: it is changed to the thalweg point closest to the newly selected site. This update is made so that if the adult ever repeats colony site selection, as a consequence of site abandonment (Section 4.10) or re-nesting (Section 4.11), it will start looking for a new site at its current site instead of at its original arrival location. This difference could be important if the adult originally arrived where there were no nearby sites.

### 4.4 Adult mating

This action determines which unmated adults become mated and change their *adtReproductiveStatus* variables from “unmated” to “mated.” Mating is represented because adult females require an unmated male to breed.

Even though mating is in reality a decision made by terns, it is simplest to model as an action of the sites. The steps followed by each site to determine which of its adults mate are detailed in Section 8.6. The order in which sites execute this action is arbitrary because it does not affect results.

### 4.5 Nest initiation

Nest initiation is when mated females change their *adtReproductiveStatus* variable from “mated” to “laying” and create a nest. Nest initiation is executed by females that meet a number of criteria defined in the nesting readiness submodel (Section 8.7; females not meeting all criteria do nothing in this action). Females execute the action in the order in which they were created. This action includes the following steps:

- The female selects a cell in which to place her nest, using the nest site selection submodel (Section 8.8). Nest locations are tracked only by which cell they are in (*nesCellID*).

- The female's *adtBreedingAttempt* value is incremented by 1. If the female's mate is alive, its *adtBreedingAttempt* value is also incremented.
- A new nest object is created and located in the selected cell. The nest's *nesFemaleID* variable is set.
- The clutch size is determined via the clutch size submodel (Section 8.3).
- The nest's variable for incubation duration is set by drawing a random number from a normal distribution with mean and standard deviation equal to parameters ***nestIncubationDurationMean*** and ***nestIncubationDurationSD***, and then rounding it off to the nearest integer.
- The female's *adtReproductiveStatus* variable is changed from "mated" to "laying."

The incubation parameters ***nestIncubationDurationMean*** and ***nestIncubationDurationSD*** have standard values of 21 and 1.5 days. These values were provided by Terry Shaffer, U.S. Geological Survey (USGS) Northern Prairies, from an extensive database of unpublished data on ILT incubation durations.

#### 4.6 Egg laying

This action represents how eggs are laid over time after a nest is created. The egg laying action is conducted by female adults that have their *adtReproductiveStatus* variable equal to "laying," including those who switched to "laying" status on the current time step. These females execute the action in arbitrary order, as the order should not affect results. The action determines whether an egg is produced on the current time step, whether the egg is viable, and whether the female has finished laying all her eggs. Details are in the egg laying submodel (Section 8.9).

#### 4.7 Hatching

Hatching is a nest action; it defines when incubation is complete and chicks hatch from viable eggs. Nests execute the action in arbitrary order, as order should not affect results. Hatching occurs when the number of days between when the last egg was laid and the current date is equal to the nest's variable for its incubation duration.

When hatching occurs, one new chick is created for each of the nest's viable eggs. New chicks have their *chkMotherID* variable set to the female that

created the nest. The chick's variable for its fledging date is set to the current date plus a random number drawn from a normal distribution with mean and standard deviation equal to parameters ***chickPeriodDurationMean*** and ***chickPeriodDurationSD***, and then rounded off to the nearest integer. A value of 20 days for ***chickPeriodDurationMean*** was estimated from Thompson et al. (1997). The authors specified a SD using the range of chick period durations specified in USACE (2009) divided by 6, with the assumption that 6 standard deviations should encompass 99.7% of all values in normally distributed data.

As part of the hatching action, the nest is removed from the model, and its female's *adtReproductiveStatus* value is changed from "incubating" to "brood rearing."

In the case of a nest with no viable eggs, no chicks are produced. Instead of the nest being recorded as successful, it is treated as having experienced mortality of the type "no viable eggs" (Table 1). (The parents will then automatically either re-nest, Section 4.11, or fail to breed, Section 4.12.)

#### 4.8 Chick fledging

This action is executed by chicks, in arbitrary order. If the current date is the chick's date for fledging, the chick is removed from the model because it represents a bird now able to fly and migrate. Consequently, birds that have fledged are no longer vulnerable to chick mortality.

The *adtReproductiveStatus* of the chick's adult parents is set to "successful" and then the parents are removed from the model. (This step is ignored if the parents have already been removed because another of their chicks fledged.) Adults are therefore no longer vulnerable to mortality after their chicks have fledged.

The parameter ***manareaLastFledgingDate*** (a Julian date) is used in other actions as the last date on which chicks can successfully fledge (to determine the last dates adults can re-nest or abandon their sites; see sections 4.11 and 8.11). The parameter belongs to the management area because its value can vary among tern populations. The standard value of 244 (September 1) is based on a common assumption that ILT begin fall migration around this date. However, final hatch dates for some datasets suggest that this date could be 1-2 weeks later if late-hatching chicks receive parental care through fledging. Users may wish to increase this value.

Table 1. GUI-observable events.

Event type	Happens to	Event description (location in Section 4 where event occurs)	Detail values
Arrival	Adult	Arrival in model (4.2)	
Adult mortality	Adult	Death by mortality agent (4.9)	Type of mortality agent
Reproductive failure	Adult	Impossibility of producing a fledgling (4.12)	"Max number of failures" or "Not enough time to re-nest"
Reproductive success	Adult	First fledging of an offspring chick (4.8)	
Nest initiation	Nest	Laying of first egg in a nest (4.5)	
Nest mortality	Nest	Destruction by flooding, mortality agent, parental mortality, or parental abandonment; or hatching date achieved when there are no viable eggs (4.9).	"Flooding," type of mortality agent, "death of both parents," "parental abandonment," or "no viable eggs"
Nest success	Nest	Nest hatches $\geq 1$ egg (4.7)	
Chick arrival	Chick	Occurs for each viable egg that survives the incubation period (4.7)	
Chick mortality	Chick	Death due to flooding, mortality agents, parental mortality, or parental abandonment (4.9)	"Flooding," type of mortality agent, "death of both parents," or "parental abandonment"
Chick fledging	Chick	Occurs for each chick that survives the chick period (4.8)	

Regardless, the model allows chicks to fledge after the date specified by the *manareaLastFledgingDate* parameter. Stochastic methods for assigning the duration of nest incubation and chick periods make it possible for chicks to remain after *manareaLastFledgingDate*. Such chicks will be within a few days of fledging (unless they received an anomalously high value of incubation or chick period duration). Instead of assuming they die prior to migration, it is simply assumed they fledge and successfully migrate a few days later.

## 4.9 Mortality

Five kinds of mortality are simulated, and executed in the order of the following subsections. Flooding is executed first because it is typically either negligible or more widespread and severe than other kinds. Site abandonment is executed last because it is a consequence of other kinds of mortality.

Mortality is modeled as site actions. The order in which the different sites execute mortality is arbitrary and should have no effect on results. When



any tern object (nest, chick, adult) is killed by one kind of mortality, it is no longer subjected to the remaining kinds; hence, an individual that would be killed by two kinds of mortality dies only of the kind that is executed first.

#### **4.9.1 Flooding mortality of nests**

Since nests are immobile, any nest in a submerged cell (cell elevation less than the daily maximum WSE) is assumed to die of flooding.

#### **4.9.2 Flooding mortality of chicks**

Chicks are mobile and assumed to walk to the highest point on a site if necessary to avoid flooding. However, they cannot fly and swim poorly, so it is assumed they are killed by flooding if all cells of their site are submerged.

#### **4.9.3 Predation and disturbance mortality**

This action represents mortality due to predators and human disturbance. “Mortality agents” each represent one source of mortality (e.g., a nest predator or an ORV). The number of mortality agent types and the characteristics of each (how often they occur, how much mortality they cause on which tern life stages) are determined by model parameters. The predation and disturbance mortality submodel (Section 8.10) includes the detailed methods.

#### **4.9.4 Mortality due to the death of both parents**

Tern eggs and chicks require care by their parents: eggs must be incubated and chicks must be fed. It is assumed that at least one parent is needed to keep nests and chicks alive. Therefore, this mortality action is executed by all nests and all chicks. They are assumed to die if neither parent is alive. This mortality is *not* applied to chicks whose parents have been removed from the model as successful breeders when their first chick fledges; Section 4.8.

#### **4.9.5 Mortality due to parental abandonment**

This mortality action is executed by all nests and all chicks. They are assumed to die if both parents have left their site via site abandonment (Section 4.10). This mortality action is separate from mortality due to the

death of both parents (Section 4.9.4), to allow users to understand whether parents were gone due to mortality vs. site abandonment.

#### 4.10 Site abandonment by adults

Each site executes an action that determines whether all adults abandon the site due to excessive mortality rates. Site abandonment is an adaptive behavior of ILT that has been described in two ways. First, adult terns arriving at a potential nesting site have been observed to leave the site and nest elsewhere, apparently because they decided that the first site is too risky (Burger 1984). Second, even after nesting, all the adults at a site may leave the site and nest again elsewhere, presumably because mortality reaches a level where abandoning nests or chicks for another site has higher expected reproductive success. The site abandonment submodel is described at Section 8.11.

If all adults abandon a site, their *adtReproductiveStatus* variable is reset to “unmated” and, on the following day, they execute the colony site selection action (Section 4.3) to select a new nesting site. However, for terns selecting a new site after abandoning one, the abandoned site is excluded as a potential new site. If a female tern abandons a site prior to laying eggs, this does not affect the number of days she must wait before egg-laying (Section 8.7): the first date on which a female can create a nest—either her first or subsequent ones—does not change if her site is abandoned before nesting. Any nests and chicks at a site abandoned by adults will die on the following day due to parental abandonment (Section 4.9.5).

#### 4.11 Re-nesting

Re-nesting is an action of adult terns that represents their ability to create a new nest of eggs, perhaps at a different site, if their nests are destroyed or if all of their offspring have died. Adult terns execute re-nesting if all of the following conditions are met.

- If female, the adult’s *adtReproductiveStatus* variable is “incubating” or “brood rearing”;
- If male, *adtReproductiveStatus* is “mated” and the mate either (a) has *adtReproductiveStatus* equal to “incubating” or “brood rearing,” or (b) is dead;
- There are no live nests or chicks that have the adult as a parent;

- There is enough time for new nests to hatch and chicks to fledge: the current date plus the parameters ***adultMinRenestingInterval***, ***nestIncubationDurationMean***, and ***chickPeriodDurationMean*** is less than the date specified by the parameter ***manareaLastFledgingDate***; and
- The adult's state variable for breeding attempt number is less than the adult parameter ***adultMaxNumBreedingAttempts***.

To re-nest, both adults have their *adtReproductiveStatus* variable reset to “unmated” and, on the following day, execute the colony site selection action (Section 4.3) to select a new nesting site. Real terns may remain mated through re-nesting (Thompson et al. 1997) and groups of terns that fail often re-nest together (Massey and Fancher 1989). However, these behaviors should not be imposed, but both adults should simply be allowed to repeat the colony site selection and mating behaviors. In simulations, groups of adults that re-nest may select the same new site and the same two adults may mate again with each other.

The parameter ***adultMinRenestingInterval*** is the minimum number of days between nesting attempts, reflecting the time needed for adults to rebuild energy reserves etc. before starting a new clutch. Its standard value is 5 days, on the basis of Massey and Fancher (1989) and Lingle (1993).

The parameter ***adultMaxNumBreedingAttempts*** is the maximum number of clutches a female can lay per year. Thompson et al. (1997) noted that female Least Terns can nest up to 3 times in a breeding season. However, most empirical studies refer to two distinct waves of nesting (Massey and Fancher 1989, Kress and Hall 2002). No documentation of individual females nesting 3 times could be located in the literature. Since this parameter can have a strong effect on reproductive success in years with considerable nest failure, the authors selected a default value of 2 for this parameter to avoid overestimation of reproductive success.

#### 4.12 Reproductive failure

Reproductive failure is an action to remove adults that fail to produce live offspring during a single breeding season. Adults execute reproductive failure if all of these three conditions are met:

- Their *adtReproductiveStatus* variable is “incubating” or “brood rearing” if female, or “mated” if male;

- There are no live nests or chicks that have them as parents; and
- They cannot re-nest due to any of these reasons;
  - There is not time for new nests to hatch and chicks to fledge: the current date plus parameters ***adultMinRenestingInterval***, ***nestIncubationDurationMean***, and ***chickPeriodDurationMean*** is equal to or exceeds the parameter ***manareaLastFledgingDate***.
  - Their state variable for breeding attempt number is equal to the adult parameter ***adultMaxNumBreedingAttempts***.

The breeding failure action simply removes the adults from the model with their *adtReproductiveStatus* variables set to “failed.”

### 4.13 Output

The final action is to record output for observation via the GUI or as file output for later analysis. In fact, several kinds of output are produced at different times in the model schedule; details are provided in Section 5.8.

## 5 Design Concepts

The ODD protocol includes a description of how the model implements the following design concepts. These design concepts provide a standard way of thinking about and documenting the aspects of an individual-based model that are not captured well in equations.

### 5.1 Emergence

The main outputs of this model are the number of fledglings produced. Some important secondary results are how nests and fledglings were distributed among sites (e.g., which sites were and were not productive), and the effects of various mortality sources. These results emerge from the main behaviors of adult terns: selecting nesting sites, selecting habitat cells to place nests, and re-nesting after nest or brood failure. The results also can emerge from one adaptive behavior of the tern colonies: deciding whether the adults at a nesting site should abandon it due to high mortality rates. These behaviors, and the subsequent consequences for reproductive success, are strongly affected by habitat conditions: the number, size, location, and characteristics of the sandbar sites; how sandbar characteristics are affected by daily river flows; and the types and intensity of predation and human disturbance.

### 5.2 Adaptation

Two of the main adult tern behaviors are adaptive in that individuals identify and compare alternatives: selecting the site they nest on (including when they re-nest) and selecting the cell at that site where they place a nest. These behaviors are modeled as indirect fitness-seeking traits, assuming that each of several habitat variables of sites and cells affects the expected reproductive success of terns. Terns evaluate habitat to choose both nesting sites and specific cells at sites to place their nests in consideration of this expectation.

The model includes one adaptive behavior of tern colonies (the terns at one nesting site; Section 5.7): site abandonment. This behavior is represented as a direct fitness-seeking trait, with a site's adult terns all deciding to abandon the site if a specific indicator of expected reproductive success is not met.

### 5.3 Objectives, learning, prediction

The adaptive traits of individual terns do not use explicit decision objectives, learning, or prediction. However, the site abandonment trait made collectively by all adults at a site is based on a specific objective. A site is abandoned if the expected number of fledglings produced there in the current season (a function of the number of adults, nests, and chicks at the site and their current mortality rates) falls below the number of fledglings expected if the adults all leave and re-nest elsewhere.

### 5.4 Sensing

Assumptions are made about tern sensing in two traits. In their colony site selection trait, terns sense and evaluate sites that are within a limited distance (specified by parameter ***adultSiteSelectionDistance***), either upstream or downstream of the point where they first arrive at the river. In the colony site selection and nest site selection traits, adult terns are assumed to be able to sense the habitat quality of all sites in within the specified distance of the arrival point and all cells at the selected site; this habitat quality is a function of variables such as distance to vegetation and forest, and elevation above the water surface at daily peak hydropower flow (Section 8.1). The habitat quality variables are all easily observed; terns can see evidence of daily peak water elevation such as wet sand or wrack lines indicative of recent higher flows.

### 5.5 Interaction

The model assumes relatively little interaction among terns. For example, there is no competition for resources other than nesting habitat, which is typically abundant at nesting sites. Adult terns must find a mate before nesting.

Mortality due to predation and disturbance is modeled as a direct interaction (killing) between an explicit mortality agent (predator, etc.) and terns. Mortality agents also cause indirect mortality of nests, through the cessation of care by adults that are killed or that abandon nests due to disturbance from mortality agents (Section 4.10). Site abandonment can also cause adult terns to avoid nesting on a site that might otherwise provide high success.

## 5.6 Stochasticity

The following processes are partially stochastic. In all cases, the purpose of stochasticity is simply to impose a realistic level of variation when the variability is felt to be essential, without modeling the causes of variation.

- Determining the number of adults arriving from migration per day, though the mean arrival rate varies deterministically through the season.
- Assigning the location where adults of the “disperser” type arrive at the management area (section 8.2).
- Setting clutch size, egg viability, incubation duration, and the duration of the chick period.
- Setting the sex state variable for each adult tern.
- Determining whether a new mortality agent appears each day at each site, and how long the agent stays at the site.
- Setting the number of nests, chicks, or adults that each mortality agent kills each day.
- Selecting the cell in which a tern places its nests (from cells with habitat quality above a threshold).

## 5.7 Collectives

The model’s site abandonment trait is executed collectively by all the adult terns at a site (colony). This trait affects all the individuals at the site (determining whether adults leave and re-nest, and whether the nests and chicks die as a consequence) and is a function of colony—not individual—characteristics such as number of terns present and the site’s mortality rate. Consequently, the colonies act as collectives for this trait.

## 5.8 Observation

Model observation takes place primarily through a GUI at <http://www.leasttern.org>. GUI tables and graphics that permit model observation are constructed via queries of *Postgres* database tables where detailed results are recorded as the model executes. Four kinds of results are logged to the database. First, site-specific summaries of habitat conditions and the number of model objects at each site at the end of each day are logged to the **tblSiteSummary** database table. Second, specific events that occur to specific model objects (an individual adult, nest, etc.) on a specific date are logged as they occur to the **tblEvents** database table; the date and identifier of the object are recorded as part of each event. One “detail” is also recorded for each event from a

discrete set of detail values that are used to describe the cause of each event type. Table 1 summarizes the 10 different event types, the kind of model objects that each of these events happen to, where in the model schedule they occur, and the potential “detail” field values that depict the event’s cause. Third, state variables for all model objects (adults, nests, chicks, and mortality agents) are stored in object-specific tables (**tblAdult**, **tblNest**, **tblChick**, and **tblMortalityAgent**) as individual model objects are created. Some state variables for individual model objects change across the breeding season (e.g., the *adtReproductiveStatus* state variable for adults, the *nesNumViableEggs* state variable for a nest). At the end of a simulated breeding season, these tables reflect the terminal state variables of each object (e.g., the value for each adult’s *adtReproductiveStatus* state variable is either “successful” or “failed”). Finally, at the end of each simulated breeding season, a number of summary metrics are calculated for each site, each reach, and the entire management area and logged to the (**tblResults**) table in the database. Summary metrics are listed in Appendix C.



## 6 Initialization

When the model is started, two main initialization steps are executed. First, model habitat is initialized by creating the management area, sites, and habitat cells (Section 6.1). Second, adult terns are created and added to the model (Section 6.2).

### 6.1 Habitat initialization

Habitat initialization creates the management areas, sites, and cells. The number of these entities, and all their state variables—except those set by the daily habitat update action (Section 4.1)—are read as input from the database.

Habitat cells are loaded from database tables created via GIS (Lott and Wiley 2012). For example, on the Arkansas River below Keystone Dam, site inputs have been created for several sets of sandbar habitat conditions observed in different years. Each of these is considered a unique Habitat Input Set in the database (**pltblHabitatInputSet**).

- 2008 sandbars (n = 32), based on field measurements after major habitat forming flows in 2007 and 2008 (e.g., excellent regional habitat conditions) reported in Lott and Wiley (2012)
- 2005 sandbars (n = 25), which were generated in GIS to represent the highly degraded conditions that existed prior to the high flows of 2007 and 2008
- Potential restoration sandbars (n = 17), which were generated in GIS to allow users to add restoration sandbars to the model to see the effects of different approaches towards habitat creation

The subset of sites to be included in any one model run or simulation experiment is specified by the model parameter *manareaSiteCodes*, which can be specified by users in the GUI (see GUI documentation for details). In the GUI, users first select between one of the available Habitat Input Sets. Then, users may modify the final list of sites that will be initialized in one of 3 possible ways (or not at all):

- One or more sites from the default list of sites for each habitat input set may be removed (e.g., to simulate lesser habitat availability).

- One or more sites from the list of potential restoration sandbars can be added (e.g., to simulate different scenarios of habitat creation).
- One or more sites (either default sites or restoration sites) may be excluded from selection by terns (e.g., to simulate the unavailability of some sites, despite suitable physical habitat conditions, due to heavy disturbance).

The value of *manareaSiteCodes* used in any model run is stored in the metadata describing the run.

## 6.2 Adult tern initialization

The model uses parameters for population size and breeding phenology to determine how many total adult terns arrive in the management area from spring migration and the dates that each arrives. This is done during initialization by executing the adult initialization submodel (Section 8.2), which also initializes adult tern state variables. Terns are actually inserted into the model over time by the adult arrival action (Section 4.2).

## 7 Time-Series Input Data: Daily Flows

The model's only time-series inputs are site-specific peak daily flows for each ILT breeding season (**tblDailyFlow**). Flow inputs are site-specific to account for how daily peak flows vary by distance below dams on regulated rivers due to attenuation of daily hydropower generation peaks as well as tributary inputs (Lott and Wiley 2012). Site-specific flows are necessary to update site-specific habitat variables (Section 8.1).

Like habitat inputs, more than one set of peak daily flow inputs may be available for each management area (e.g., representing different reservoir operation strategies or flows before and after a dam was in place). Therefore, each set of site-specific flow inputs is assigned to a specific Flow Input Set (**pltblFlowInputSet**). When users specify flow inputs for simulations in the GUI, they must first select which flow input set they will use from a list of possible sets for each management area. Each flow input set contains >1 “annual flow input.” An “annual flow input” is a time series of peak daily flows for one breeding season. Properties of annual flow inputs are stored in the database table **tblWaterYear**.

Each annual flow input belongs to a specific “water year category,” represented by the field *wyrCategoryID*. Water year categories are groups of annual flow inputs with flow patterns that are similar in how they affect tern breeding (e.g., low water years, high water years, or years with mid-season flooding). Water year categories vary among management areas due to regional differences in precipitation, runoff, and dam operations. Water year categories specific to each management area are defined in the database table **tblWaterYearCategory**. See Lott et al. (2012b) and Lott and Wiley (2012) for more details on how water year categories may be specified. When users specify flow inputs for a batch of model runs, they may wish to specify inputs randomly from all possible inputs, or they may wish to specify inputs by water year category (e.g., randomly from among only low water years).

A group of flow inputs (e.g., 24 different annual flow inputs randomly selected from all possible inputs) is stored in the database as a “Flow Input Group.” Properties of flow input groups (e.g., *wygName*, *wygUserId*, *wygWaterYearGroupID*) are stored in the table **tblWaterYearGroup**.

The complete list of annual flow inputs belonging to each flow input group is stored in the database table **linkWaterYearGroupWaterYear**. Flow input groups can be specified once and re-used in future simulation experiments.

## 8 Submodel Details

This section provides details on the “submodels” (algorithms for specific processes or events, which can be designed, tested, and calibrated separately) that are too complex to describe fully in the Section 4 model overview. These details include a full description of each submodel and its parameters and, where appropriate, the literature, data, testing, etc. used as a basis of the submodel’s design. Some submodels were tested in enough detail so that additional testing is described in Lott et al. (2012a). Subsection 8.11 does not describe a particular submodel but the methods used to generate pseudorandom numbers for the stochastic model functions.

### 8.1 Habitat update submodel

This submodel is executed by each site, each day. The first step is for the site to read its daily maximum flow from input and calculate the maximum water surface elevation (WSE) from site-specific stage-discharge relationships. Development of these relationships is site-specific and should be documented for each application. WSE is calculated using the equation:

$$z = \exp \left\{ a + b \ln Q + c (\ln Q)^2 \right\}$$

where  $a$ ,  $b$ , and  $c$  are empirical coefficients input as site variables *sitFlowToElevA*, *sitFlowToElevB*, and *sitFlowToElevC*;  $z$  is WSE, and  $Q$  is the peak flow (cfs) for that day.

Second, cell freeboard values are calculated by subtracting the WSE from the cell elevation. All cells with cell freeboard values  $< 0$  are inundated. This approach neglects the possibility of cells being protected from inundation by being completely surrounded by higher cells, or of water being trapped in such low cells as WSE goes down.

Third, habitat variables are updated. The first set of habitat variables updated is cell quality, a continuous habitat quality index for each cell, which depends on WSE. Once each cell at a site has its cell quality value updated, the site’s habitat quality variable *ssmHighestQuality* is set to the highest cell quality value of the site’s cells (*ssmHighestQuality* is the maximum cell quality of the site, not the average).

Cell quality is the product of logistic function values for five habitat variables, which are defined in Table 2 and illustrated in Figure 1. Logistic functions are used because they produce outputs that vary continuously over the range of 0-1 and reflect how the quality function can be insensitive to habitat variables at low and high values but sensitive at intermediate values. Note that this measure gives cells that are submerged or vegetated quality values *near but not equal to* 0.0. The default parameter values for distances to forest, bank, and vegetation in Table 2 came from the authors' analysis of nest location and habitat data collected on the Missouri River between 1999 and 2006 (USACE 2011).

The logistic parameter values for cell freeboard are based on the observation that terns tend to create nests on dry rather than wet sand. Since capillarity (the upward wicking of water through sand) varies by site due to differences in soil substrates, the 0.1 and 0.9 parameter values are based on the approximation that most locations within 0.5 ft of the peak daily WSE are likely to be wet. Some locations between 0.5 and 1.0 ft of the peak daily flow WSE are also likely to be wet, but locations >1 ft above the peak daily flow WSE are likely to be dry.

The logistic parameter values for freeboard above peak hydropower are based on two approximations: 1) cells with freeboard >1 foot at peak hydropower flow remain dry during the most frequently occurring breeding season flows, and 2) cells with at least 3 ft of freeboard above the peak hydropower flow are generally safe from moderate release/runoff events (e.g., on the Arkansas River a freeboard of 3 ft at peak hydropower flows indicates a cell that is not inundated until flows of ~30,000 cfs, which do not occur in all years). The value of ***adminQualFreeboardAtMinSuitableFlow09*** should be re-evaluated considering stage-discharge relationships and breeding season hydrographs for each management area the model is applied to.

Once each cell has had its habitat quality index updated, site variables that depend on quality of the site's cells are updated. These site variables are the area (in acres) in four different habitat quality categories, evaluated by summing the area of cells that meet the criteria defined below.

*ssmSuitableAcres* is the area of "suitable habitat," cells where terns could potentially nest, excluding only cells with habitat characteristics that would essentially preclude tern nesting. This suitable habitat includes cells

Table 2. Nesting habitat quality parameters.

Habitat variable	Value at which logistic function is 0.1 (parameter name)	Value at which logistic function is 0.9 (parameter name)
Distance to forest edge ( <i>celDist2ForestEdge</i> )	400 ft ( <i>adminQualDist2ForestEdge01</i> )	600 ft ( <i>adminQualDist2ForestEdge09</i> )
Distance to bank ( <i>celDist2Bank</i> )	100 ft ( <i>adminQualDist2Bank01</i> )	400 ft ( <i>adminQualDist2Bank09</i> )
Distance to nearest vegetation ( <i>celDist2Veg</i> )	50 ft ( <i>adminQualDist2Veg01</i> )	500 ft ( <i>adminQualDist2Veg09</i> )
Freeboard above the minimum suitable flow	1.0 ft ( <i>adminQualFreeboard AtMinSuitableFlow01</i> )	3.0 ft ( <i>adminQualFreeboard AtMinSuitableFlow09</i> )
Cell freeboard	0.5 ft ( <i>adminQualFreeboard01</i> )	1.0 ft ( <i>adminQualFreeboard09</i> )

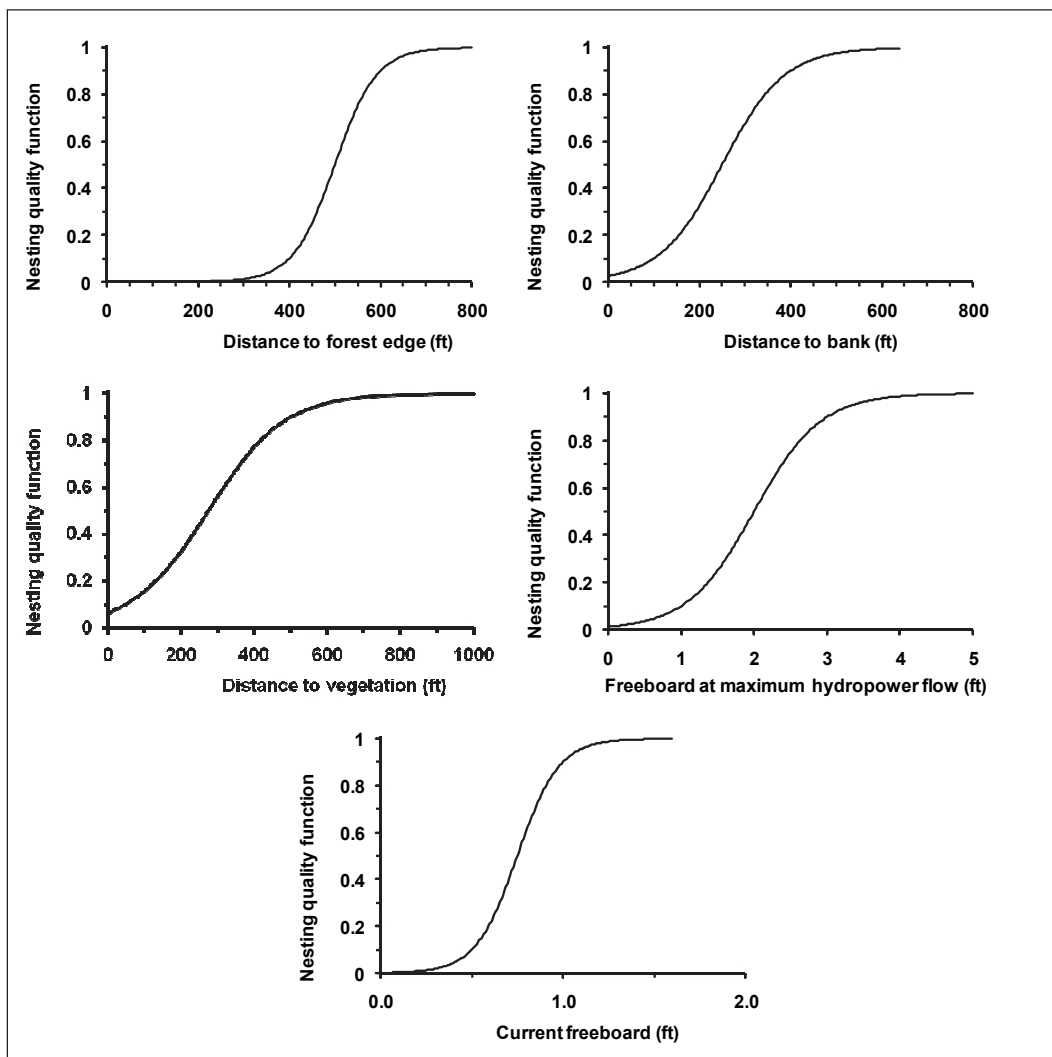


Figure 1. Habitat quality functions.

that meet three criteria: 1) they are not inundated at the current daily maximum flow; 2) they are not inundated at a daily maximum flow typical of normal hydropower production during low-runoff conditions, specified by the site variable *sitMinSuitableFlow*; and 3) they are free of vegetation (*celVegetation* = 0).

If a cell is suitable, it can be assigned to one of three habitat quality categories: low, medium, or high. The site variables *ssmDisplayLowQualityAcres*, *ssmDisplayMediumQualityAcres*, and *ssmDisplayHighQualityAcres* are the area of cells in those three categories. These variables are used to provide more resolution in the display of how habitat varies among sites or within sites among flows. A low quality habitat cell has a habitat quality less than the parameter ***adminDisplayMediumQualityLowerThresh***, which has a standard value of 0.06561, the value when one of the five habitat functions is 0.1 and the remaining four are 0.9. This threshold assumes that a low value for any one habitat function, by itself, reduces habitat quality dramatically. A high quality habitat cell has habitat quality higher than the value of parameter ***adminDisplayHighQualityLowerThresh***, which has a standard value of 0.59. This is the value of the index when each of the five logistic functions has a value of 0.9. This “high quality” threshold can still be met when one function has a value as low as 0.7, if the other functions are considerably greater than 0.9. Habitat quality values between the two threshold parameters are considered medium quality cells.

## 8.2 Adult initialization submodel

The adult initialization submodel determines how many adult terns arrive, and the day each arrives from spring migration in each management area and initializes his or her state variables. Unlike the other submodels, this one is executed once when the model is initialized so that the number arriving each day and the total number of adults is known from the start of a simulation. The submodel has two parts: initialization of arrival dates and state variables.

### 8.2.1 Arrival dates

This part of the submodel determines how many adults arrive from migration on each date. It is designed to be simple and easily parameterized to reproduce observed characteristics of the timing of breeding. The approach is to:



- Model the arrival rate (expected rate of arrivals per day) as a triangular function of the Julian date and the total number of adult terns arriving over the whole breeding season. For each management area, the first and last days of arrival and the peak arrival day are calculated from parameters that define first, last, and peak dates of nest initiation, as well as a parameter that defines the time lag between arrival and nest initiation. These calculations are described below. The arrival rate on any day is simply the elevation of the triangle at that day.
- Determine the actual number of adults arriving on a day by drawing a random integer from a Poisson distribution with its rate parameter set to that day's expected number of arrivals. Using the Poisson distribution has two purposes: it introduces some "natural" variability into arrivals, and it produces an integer number of arrivals from the non-integer expected arrival rate.

The arrival submodel uses four variables to define the triangular distribution. The first variable is the management area parameter ***manareaNumAdults***, the approximate number of adults returning to the management area. (The number of adults arriving per day is stochastic, so the exact total arriving in a model run varies stochastically with the value of ***manareaNumAdults*** as the mean.) The other three variables are:  $T_S$ , the date of first arrival;  $T_P$ , the date of peak arrival; and the date of last arrival,  $T_E$ .

Due to the fact that arrival dates are almost always estimated from observations of nest initiation dates (the date on which the first egg is laid in a nest), the model calculates  $T_S$ ,  $T_P$ , and  $T_E$  from parameters that represent the first, peak, and last date of nest initiation. These management area parameters are ***manareaFirstNestDate***, ***manareaPeakNestDate***, and ***manareaLastNestDate***. The arrival date variables are determined by subtracting the adult parameter for the time between arrival and nesting (***adultMinDaysArrivaltoEggLaying***; Section 8.7) from these parameters. Users must be very careful to understand that arrival dates are determined from parameters related to nest timing.

The arrival rate for any day during the arrival season is calculated using these equations for a triangular distribution:

$$R_p = \frac{2N}{T_E - T_S}$$

$$\text{If } t \leq T_p : R_t = R_p \frac{t - T_s}{T_p - T_s}$$

$$\text{If } t > T_p : R_t = R_p \frac{T_E - t}{T_E - T_p}$$

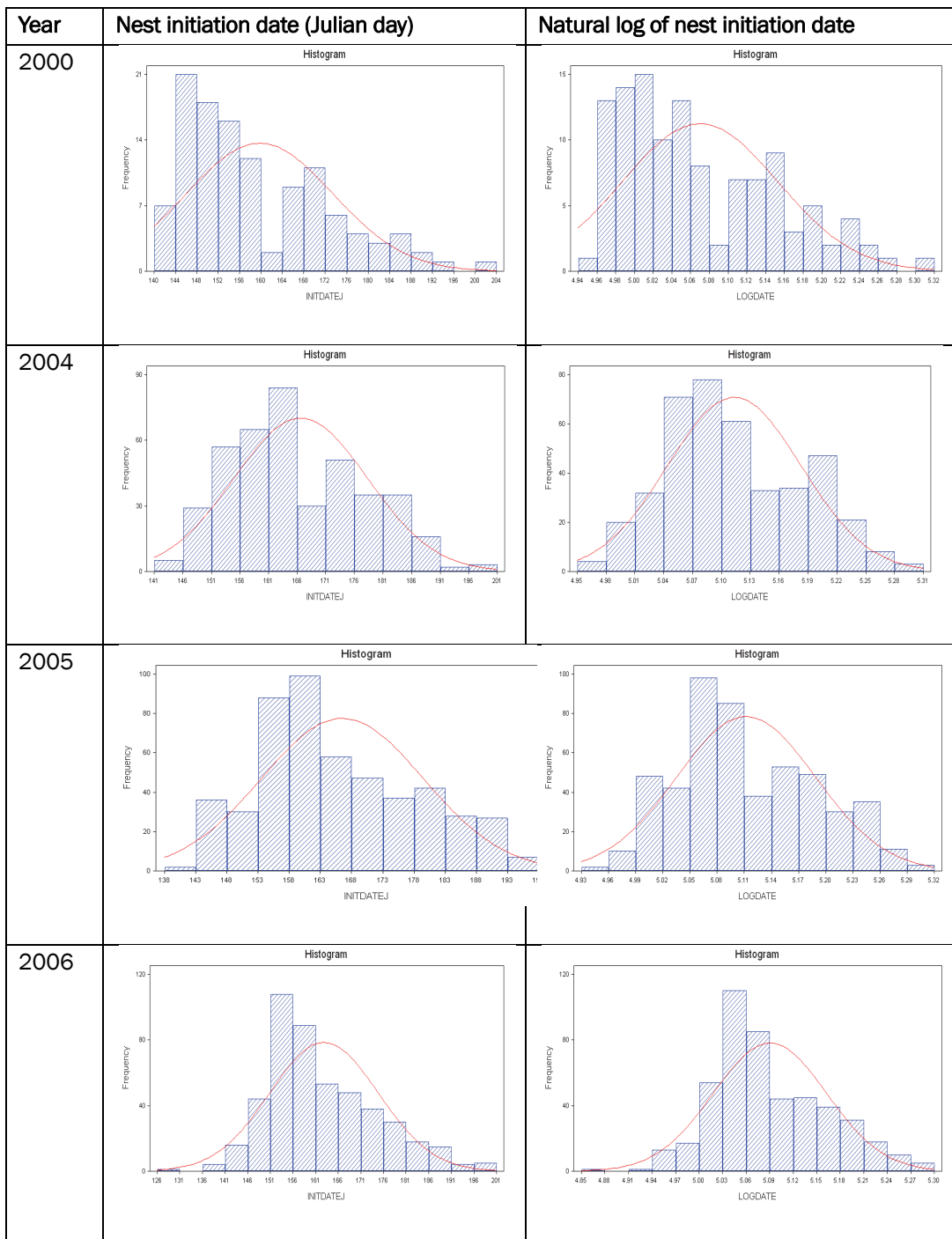
where  $R_p$  is the maximum arrival rate,  $N$  is ***manareaNumAdults***,  $t$  is the current Julian date, and  $R_t$  is the daily rate of adult arrivals.

The number of adults actually arriving in the model on a date between the start and end of the arrival period is drawn from a Poisson distribution with its rate parameter set to  $R_t$ . It should be noted that on the first ( $T_s$ ) and last ( $T_E$ ) days of this arrival period, the value of  $R_t$  is zero (the height of the triangular distribution is zero at its first and last vertices). Hence, adult terns actually arrive after  $T_s$  and before  $T_E$ .

The authors tested this submodel using nest initiation date data from the Missouri River for 1999 to 2006. During this period on the Missouri River, nesting habitat was abundant and flooding infrequent, so few terns likely nested more than once. The nest initiation dates were histogrammed for each year (results for several example years are in Figure 2). These data indicate:

- Nesting dates are generally skewed toward earlier than the mean, though they do not clearly fit a log-normal distribution well.
- A triangular distribution may fit the data as well as either a normal or log-normal distribution, though it may overestimate the amount of nesting near the start and end of the period.
- Nesting dates changed among years. Similarly, it is to be expected that different values would be obtained if nest initiation data were summarized for different locations.

While developing the arrival date submodel, the authors used draft parameter values for arrival dates that were informed by nest initiation data from the Missouri River (Table 3). After an extensive literature review, the authors were able to specify standard parameter values for ***manareaFirstNestDate***, ***manareaPeakNestDate***, and ***manareaLastNestDate*** based on many additional data sources (see Appendix A). Nest initiation dates from studies throughout the whole range of ILT differed very little from the dates reported below for the Missouri River from 1999-2006 (Thompson et al. 1997).



**Figure 2. Distributions of nest initiation dates observed on the Missouri River, 2000–2006 data. The X axis is Julian date; each bar represents four days. In the left graphs, the Y axis is the number of nests initiated during the four days, with a best-fit normal distribution curve. The right column histograms the natural log of the nest initiation date to show how well a log-normal distribution fits the data.**

Table 3. Missouri Basin nest initiation data relevant to arrival parameter estimation.

Year	First nest initiation date	Last nest initiation date	Peak nest initiation date
1999	145	200	150
2000	141	204	146
2001	143	198	156
2002	130	197	155
2003	138	199	154
2004	142	201	163
2005	139	203	160
2006	128	200	154

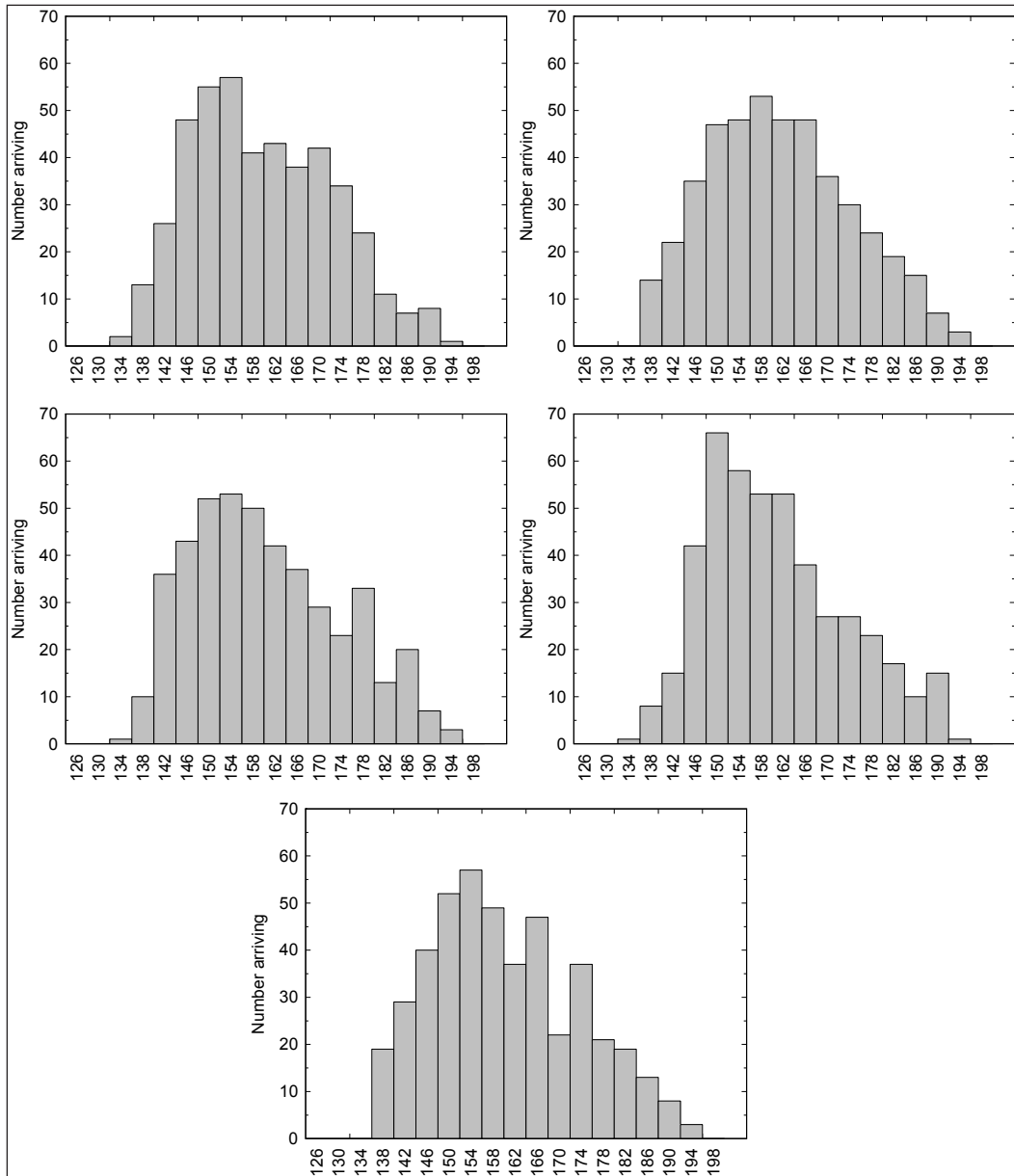
To illustrate the level of variability in the arrival submodel, the results of five replicate simulations are presented (Figure 3), in comparison to observed nest initiation date distributions (Figure 2). This analysis indicates that the model captures the general shape and level of variability in the observations. However, the model may not capture the observed low frequency of very early and very late nests well; it is not clear how important those extreme date nests could be to the model.

### 8.2.2 State variable initialization

After arrival dates are determined, the adults are created and assigned their state variable values. *adtReproductiveStatus* is set to “unmated” and *adtSex* is determined by a Bernoulli trial with 0.5 probability of being female. The value of the state variable *adtBreedingAttempt* is set to 0 for both males and females.

Adults are also assigned a value for their arrival location state variable. This is a two-step process because the model treats adult terns as having one of two migration strategies. “Returners” are adults assumed to have nested (or been born) the previous year in the management area they now return to, and to be seeking nesting sites near the one they occupied the previous year. “Dispersers” are assumed to be using the management area for the first time and consequently have no tendency to return to a particular part of it.

The fraction of adults that are dispersers is set by the parameter *manareaFracDispersers*, which has a value between 0.0 and 1.0. The number of dispersers is calculated by multiplying this parameter by the total number of adult terns and rounding the result to an integer. This number of



**Figure 3. Five replicate simulations of adult tern arrival dates, differing only in the random Poisson distribution draws. The X axis is the Julian date of the start of each four-day interval. Bar height is the number of simulated terns arriving during the interval. Parameter values: *manareaFirstNestDate* = 138, *manareaPeakNestDate* = 155, *manareaLastNestDate* = 200, *manareaNumberAdults* = 450, and *adultMinDaysArrivalToEggLaying* = 7.<sup>1</sup>**

adults is assigned an arrival location by randomly selecting one point on the management area’s list of thalweg points (Section 3.1). Little information is available to inform the value for this parameter. Therefore, the authors used

<sup>1</sup> The parameter values in Figure 3 reflect means of the Missouri River data reported in Table 3. Final parameter values for version 1.0 of TernCOLONY were based on a more extensive literature review (which is reflected in the notes to Appendix A).

this parameter in calibration of colony site selection, which produced a standard value of 0.15.

The remaining adults are returners. A table input to the model as part of a Habitat Input Set (Section 6.1) defines a list of locations (as x, y coordinates within the river channel) where the returners are assumed to have nested or been born the previous year (an example is found in Table 4). The table also specifies what fraction of the returner population came from each such previous-year location. The model calculates how many returners came from each of the previous-year locations by multiplying this fraction by the total number of returner adults and rounding the result to an integer. For each previous-year location, this number of adults has its arrival location set to the thalweg point closest to the previous-year location.

The model separately randomizes the adult terns' arrival dates and their arrival locations. Therefore, there should be no consistent correlation between when adults arrive and where they arrive.

**Table 4. Example previous-year location input (from the Keystone Reach, Arkansas River).**

X coordinate of previous-year nest site	Y coordinate of previous-year nest site	Fraction of adults
2558406.00888	1027825.62756	0.31
2573990.45648	981047.94512	0.01
2590482.18078	962984.77478	0.04
2631949.45984	946642.09193	0.02
2644939.20656	943530.64086	0.01
2655641.41086	946764.24783	0.05
2664856.96104	948415.13466	0.01
2666278.12800	945898.51871	0.02
2665796.85765	936036.66609	0.04
2665234.29177	933840.42846	0.02
2667518.19124	917729.65323	0.12
2668846.50695	907210.46350	0.04
2679539.74830	895629.13390	0.03
2691190.84581	900508.80407	0.02
2697202.25463	901869.14741	0.05
2707500.15632	906690.60004	0.14
2713490.44733	906712.96274	0.05
2744915.86844	913586.47111	0.01

### 8.3 Adult clutch size submodel

This submodel determines the clutch size (number of eggs in a nest) of a female tern. Least Terns typically produce clutches of 1-3 eggs (rarely 4), and mean clutch size can vary over time and among colonies (Szell and Woodrey 2003). Clutch sizes may be smaller when females re-nest in the same season (Hill 1985, Lingle 1993), or later in the season when less experienced breeders are attempting to breed for the first time (Thompson et al. 1997), but the model does not now represent that potential variability.

Clutch sizes are determined stochastically, using two parameters that define the likelihood of a clutch having only one or two eggs. The parameter ***adultClutchProb1Egg*** is the probability of a clutch having one egg, and ***adultClutchProb2Eggs*** is the probability of two eggs. The authors set default parameter values of .1 (for 1-egg clutches) and .42 (for 2-egg clutches) by calculating the average proportion of 1- and 2-egg clutches from 21 sampling year/site combinations at Salt Plains National Wildlife Refuge (Hill 1985), the Platte River (Kirsch 1990), and the Mississippi River (Szell and Woodrey 2003). All three of these studies are from the interior population of Least Terns, in which 2- and 3-egg clutches are common (Thompson et al. 1997). If this model is applied in coastal management areas, where 3-egg clutches are less common (Thompson et al. 1997), these parameter values should be adjusted.

Clutch size is determined by drawing a uniform random number between zero and one. If this number is less than ***adultClutchProb1Egg***, then the clutch size is one; if the random number is less than ***adultClutchProb2Eggs*** plus ***adultClutchProb1Egg***, the clutch size is two; otherwise, the clutch size is three.

### 8.4 Adult site identification submodel

The submodels for site identification and colony site selection by adult terns were designed by testing the ability of a variety of alternative submodels to reproduce observed patterns of site use. That pattern-oriented trait development process is documented in Lott et al. (2012a) and the resulting submodel is described here. The most essential results of the trait development work were that observed patterns in site use and colony size were only reproduced when (a) each tern was selected from among a limited subset of sites instead of evaluating all the sites in a reach, and (b) sites were selected

(from among the subset) considering some measure of habitat quality, which may also include the number of unmated adults (Section 8.5).

The site identification submodel defines which sites a newly arrived (or re-nesting) adult considers as a potential nesting site. It considers the possibility that no sites are available, either in the region of arrival or in the whole management area. If no sites are available near where a tern arrives from migration, it is assumed (on the basis of field observations) to continue to search for sites near its arrival location for a number of days, waiting for sites to become exposed as high flows recede, before expanding its search area. The following steps are used:

- The tern is assumed to arrive at a location (its arrival location state variable) along the management area's thalweg. This location is set when the tern is initialized (Section 6.2).
- All sites (except those excluded in the following step) within a distance equal to the parameter ***adultSiteSelectionDistance*** (ft), centered at the tern's arrival point, are considered as potential nesting sites. (In other words, the tern considers all sites within half this parameter's value in both directions from its arrival point.) This distance is measured not as a straight line but as length along the thalweg. The standard value for ***adultSiteSelectionDistance***, estimated from calibration of colony site selection, is 10,000 ft.
- In the previous step, sites are not considered as potential nesting sites if they were not among those selected for inclusion during the current simulation (Section 6.1), or if they lack any exposed suitable habitat cells.
- If no sites are identified using the above steps, the tern does not complete site identification and colony site selection on the current day (with an exception explained in the following step). Instead, the tern stops and repeats this action the following day. The tern's variable for the date when it arrives in the management area remains set to the first date on which it looks for a site, so the days spent waiting for a site to become available count toward the number of days between arrival and nesting (Section 8.7).
- However, if the number of days between the current day and the tern's arrival day exceeds the parameter ***adultSiteSelectionWaitDays*** then the tern instead identifies the one site that is nearest (in either direction) to its arrival location, excluding those sites not included in the current simulation or sites with non-positive values of



- ssmSuitableAcres*. Therefore, ***adultSiteSelectionWaitDays*** represents the maximum number of days an adult will wait near its arrival location for a site to become available before selecting a site farther away. This parameter is set to 10 days.
- If no sites are identified by the previous steps (meaning that none are available in the management area), then the tern does not select a site and tries again the following day; its arrival location does not change. The tern's variable for arrival date remains set to the first date on which it looks for a site, so any days spent waiting for any site to become available also count toward the number of days between arrival and nesting (Section 8.7).

## 8.5 Adult colony site selection submodel

This submodel represents the key behavior of how an adult tern selects the site where it will attempt to breed, from the alternative sites identified by the site identification submodel. A tern selects the site having the most unmated other terns (of either sex). If more than one site has the same, highest, number of unmated terns, one of them is chosen randomly.

If none of the sites has any unmated terns, the tern selects the site with highest value of the site variable *ssmHighestQuality* (Section 8.1).

## 8.6 Adult mating submodel

This submodel determines when adult terns become “mated.” This submodel is executed by a site, and addresses its “unmated adults,” which are adult terns with *adtReproductiveStatus* variables equal to “unmated.” These unmated adults can be newly arrived, or can be unmated due to re-nesting (Section 4.11).

As many pairs as possible (equal to the number of unmated males or females, whichever is smaller) are mated on any day when unmated adults are present at the site. For each pair to mate, one female and one male are arbitrarily selected to become mated. Whenever a pair is mated, the female and male have their *adtReproductiveStatus* variables changed from “unmated” to “mated.” Unmated adults are chosen for mating arbitrarily because which adults mate when should have no effect on results.

## 8.7 Nest readiness submodel

A female adult tern is only allowed to create a nest if the following criteria are met. The criteria apply to the first nesting attempt and to re-nesting.

- `adtReproductiveStatus` must equal “mated.”
- If the adult’s variable for breeding attempt number is zero (this is her first nesting attempt), the number of days since the adult arrived in the management area (Section 4.2) must be greater or equal to the adult parameter **`adultMinDaysArrivaltoEggLaying`**. The standard value of **`adultMinDaysArrivaltoEggLaying`**, 14 days, is based on the “two to three weeks” specified in Thompson et al. (1997). This criterion applies even if the adult has abandoned a site before nesting and is no longer at its first site.
- If the adult’s variable for breeding attempt number is greater than zero (this is not her first nesting attempt), the number of days since the previous attempt failed (the last egg or chick died) must be greater than or equal to the parameter **`adultMinRenestingInterval`**. This criterion is not affected by whether or not the adult has selected and then abandoned a site since its last nesting.
- There must be at least one cell suitable for nest creation, according to the nest site selection submodel (Section 8.8).

## 8.8 Nest site selection submodel

This submodel determines the cell where a female places her nest. This is an important decision, since it affects how vulnerable nests are to flooding. The submodel was developed and evaluated in an analysis documented in Lott et al. (2012a). Nest site selection is affected by habitat quality and a limit on nest density, and is stochastic to induce a realistic level of variability in nest elevations.

This submodel assumes a female places her nest in a cell that is chosen randomly from among all the cells meeting the criteria listed below. If there are no such cells, the female does not create a nest on the current day (Section 4.5).

- The cell’s value of the continuous habitat quality index defined in Section 8.1 equals or exceeds the product of (a) the maximum habitat quality index value among all the site’s cells, times (b) 1.0 minus the parameter **`adultNestQualityRange`**. This parameter has a standard

- value of 0.2, so this criterion means the cell must have habitat quality at least 80% of the site's maximum. This value was selected to reproduce observations that terns place nests in generally good habitat but not always closely together in the very best location.
- The cell must be of at least “suitable” quality (Section 8.1).
  - The number of nests already in the cell must be less than the cell's area divided by the parameter ***adultMinNestArea***. The parameter ***adultMinNestArea*** is the minimum area that a pair of terns needs for its nest. The standard value of this parameter is 37 ft<sup>2</sup>, which allows only one nest per cell when cell size is 6 ft (*sitCellLength*; Section 3.2). This parameter value was chosen somewhat arbitrarily so that no more than 1 nest can be created in each cell. However, nearly all studies of ILT nest spacing suggest that inter-nest distances are rarely less than 6 ft.

## 8.9 Egg laying submodel

This submodel represents the creation of eggs by female adult terns that have their *adtReproductiveStatus* variable set to “laying.” Each such adult conducts these steps each day:

- If an egg was laid on the previous day, then stop. This method represents the observation that ILT typically lay one egg every other day in clutches with >1 egg (Thompson et al. 1997).
- If an egg was not laid on the previous day, then it's possible to lay one egg by incrementing the nest's variable for number of eggs.
- Determine whether the egg is viable as a Bernoulli trial with a probability of being nonviable equal to the adult parameter ***adultFracNonviableEggs***. The standard value of ***adultFracNonviableEggs***, 0.06, is based on Kirsch (1990).
- If the egg is viable, then increment the nest's variable for number of viable eggs.
- Determine whether the number of eggs laid by the female during this nesting attempt equals the maximum clutch size. If so, the female's *adtReproductiveStatus* variable is changed from “laying” to “incubating.”

## 8.10 Predation and disturbance mortality submodel

Mortality of adults, nests, and chicks due to predators or human disturbance is modeled as a site action. The authors' approach is to model various types of predator or human disturbance mortality as individual

“agents” that are active at specific sites for a specific number of days. The types of these mortality agents and their characteristics are determined by a number of parameters (explained below). The parameters that determine what kinds of predators are potentially present, and their characteristics (how many of what life stages of terns they kill) are in the input database and cannot be changed via the GUI. Instead, the GUI lets users change parameters that control the relative intensity of mortality due to each type of agent, including setting the intensity of any agent to zero. Hence, the user can easily control which kinds of mortality agents are present and how intense their activity is, but changing the kinds of mortality agents or their characteristics requires careful parameter development and updating of the input database.

The authors describe here the specific agent types defined in the input database for the Keystone Reach application: nest predators, chick predators, adult tern predators, or ORVs. Two parameters specify the probability that an agent of each type will appear at each site on each day (see below), a single parameter specifies the average number of days that each agent stays active at a site after it appears, and three parameters specify the mean number of adults, nests, or chicks that are destroyed by a mortality agent each day that it is active at a site.

The number, location, and effects of mortality agents are then stochastic functions of these inputs and parameters. This approach models mortality not as a constant risk over time, but as events of risk that occur when a mortality agent “discovers” (is created at) a tern colony. The specific parameter values for the four types of mortality agents are provided in Appendix B. All parameters with the prefix *mam*— are defaults that require intervention in the database to change.

The parameter *mamMaxDiscoverRate* specifies the maximum rate at which each agent type will discover sites. In reality, the frequency of mortality agents appearing at sandbar sites is likely an interaction between habitat conditions, flow conditions, and predator abundance. Rather than modeling this interaction explicitly, mortality is treated as a stochastic process, with users controlling the rate at which agents occur via the parameter *magentIntensity*, a unitless control parameter that ranges between 0.0 and 10.0. This parameter specifies the fraction of the maximum discovery rate that will be used for each agent type in any given simulation. Detailed guidance for specifying this parameter is provided in

the GUI and its documentation so that users are aware of the consequences of specifying different mortality agent intensities. The effect of this parameter on mortality rates is illustrated in Figure 4. When the parameter is set to zero, mortality due to that agent type does not occur. When the parameter is 10.0, the daily probability of an agent discovering a site is set to *mamMaxDiscoverRate*.

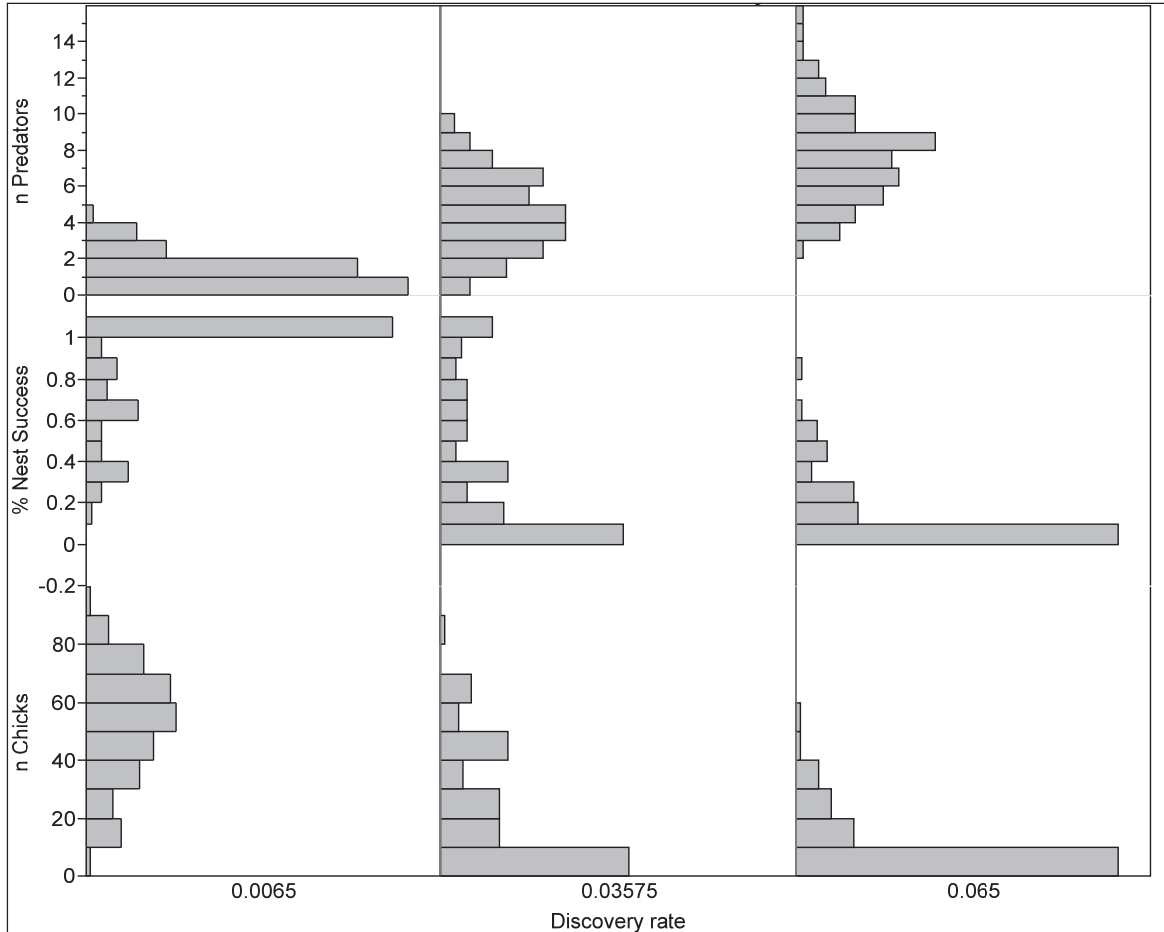


Figure 4.1 Frequency histograms illustrating the effects of nest predators on model tern colonies across 1000 simulated breeding seasons (with all other mortality processes turned off). Three different metrics are displayed on the y axis: the number of predators that discover the colony, % nest success (the percentage of nests that were not destroyed by nest predators), and the number of chicks that hatched at each colony. Three columns of histograms illustrate different values for the *mamAgentIntensity* parameter.

With *mamMaxDiscoverRate* equal to 0.022, values of 1, 5, and 10 for *mamAgentIntensity* produce the discovery rates of 0.0022, 0.011, and 0.022. One hundred adults were initialized in each simulation, resulting in an average of 50 nests per simulation (SD = 7, min = 28, max = 75 nests). Default fixed parameter values (e.g., parameters with the prefix *mam*—) for nest predators were used (see Appendix B). At *mamAgentIntensity* = 1, few predators find each site (e.g., <5 in all simulations, 0 or 1 in many simulations) and nest success and chick production are high. At *mamAgentIntensity* = 10, between 2-15 predators find each site; nest success and chick production are typically zero.

<sup>1</sup> This figure reflects simulations from version 3.0 of the model's code.

The parameter ***mamMaxDiscoverRate*** was selected and calibrated during an iterative process of testing model outputs versus patterns of ILT mortality (Lott et al. 2012a) so that user-defined values of the ***magentIntensity*** parameter reproduced mortality patterns and demographic rates observed in real tern populations. Consequently, on each day, each site determines how many new agents arrive at the site via a random draw from a Poisson distribution, the mean of which is equal to ***mamMaxDiscoverRate*** times ***magentIntensity*** divided by 10. This process is repeated for all mortality agent types defined in the input. The new agents are then created.

For each new agent, the number of days it remains at the site after its first day is determined by a random draw from a Poisson distribution with mean equal to ***mamDuration***. Predators are always active for at least their first day. If ***mamDuration*** is zero, then they will be active only on their first day. Note that more than one mortality agent of the same type can occur at a site at the same time.

After new agents are created, all mortality agents (including the just-created ones) execute the following two steps. First, each agent determines whether it disappears from the site, which can occur for two reasons. Each agent disappears when the number of days it has been active (excluding the current day, in which it has not yet done anything) exceeds (not equals) the number of days to remain at the site that it determined when created (its value of ***mamDuration***). An agent also disappears from a site if there are no more terns of the type it destroys (adults, nests, or chicks) present, either because there were none when the agent arrived or because the last of them died or left on the current day. If the number of terns of the type destroyed by the agent is currently zero, then the agent disappears from the site. This rule is based on the assumption that predators will not remain at a site if there are no more prey. It makes less sense for agents of accidental mortality such as ORVs but should have little effect on ORV mortality because those agents are present only for a few days each.

Second, each active agent determines how many adults, nests, or chicks it destroys. The order in which the agents execute this step is randomized each time step. The number killed is determined by random draws from Poisson distributions with means equal to ***mamAdultsKilled***, ***mamNestsKilled***, and ***mamChicksKilled***. When these parameters are zero, then the corresponding number destroyed is simply set to zero

instead. The specified number of adults, nests, or chicks is destroyed. They are chosen randomly from among all such objects at the site. If the number of adults, nests, or chicks present is less than the number to be destroyed by mortality agents, then they are all destroyed.

### 8.11 Site abandonment submodel

This submodel represents how the adults at a site decide, together, whether to abandon the site due to excessive mortality. Because the decision is modeled as a collective one by all adults at a site, it is a site action. The submodel is relatively complex and so is explored and analyzed in a separate document (Lott et al. 2012a).

The theoretical assumption behind this submodel is that adults abandon a site when their expected reproductive output at the site is lower than what they expect if they re-nest elsewhere. Therefore, the action requires calculating (a) expected reproductive output at the current site and (b) expected output at a new site if the adults abandon and start again.

Expected reproductive output at the current site is based on estimated daily survival rates for adults ( $S_A$ ), nests ( $S_N$ ), and chicks ( $S_C$ ). These rates are estimated from mortality events that have occurred during a past number of days; this number of days (which includes the current day, because site abandonment is scheduled after predation mortality) is determined by the parameter ***adminAbandSurvivalHorizon*** ( $H$ , in the following equations). The standard value of ***adminAbandSurvivalHorizon*** is 5 days. The daily survival rates are calculated as:

$$S_A = (N_A / (N_A + M_A))^{1/H}$$

$$S_N = (N_N / (N_N + M_N))^{1/H}$$

$$S_C = (N_C / (N_C + M_C))^{1/H}$$

where  $N$  refers to the number now alive and  $M$  refers to the number dying (of all causes) in the past  $H$  days (including the current day; e.g., if  $H = 2$ , then  $M$  is the number dying yesterday and today); and the subscripts A, N, and C refer to adults, nests, and chicks. When  $N$  and  $M$  are both zero,  $S$  is set to 1.0.

Expected reproductive output at the current site is the sum of the expected number of fledglings from (a) the current females at the site without nests (“unnested” females; those with reproductive status = “unmated” or “mated”), (b) the current nests, and (c) the current chicks. The expected number of fledglings from unnested females ( $E_{UF}$ ) is modeled as the number of females expected to survive the reproductive season times a typical number of fledglings per female. It is calculated as:

$$E_{UF} = N_{UF} (S_A)^{T_{LF}} R$$

where  $N_{UF}$  is the current number of unnested female adults,  $T_{LF}$  is the number of days left in the reproductive season (***manareaLastFledgingDate*** minus the current date), and  $R$  is the parameter ***adminExpectedFledges***, which represents the expected average number of fledglings per surviving female. The standard value of ***adminExpectedFledges*** is 1.0; Akçakaya et al. (2003) summarized observations of fledglings per female for California and Baja California populations of Least Tern and selected a value of 0.348 female fledges per female adult, corresponding to 0.70 fledges per female, to represent years without catastrophic failure.

The expected number of fledglings from current nests ( $E_N$ ) is modeled as the sum, over all current nests at the site, of their rate of survival from the current day until hatching, times the number of viable eggs in the nest, times the rate of chick survival through the complete chick period. However, because nests and chicks require adults to care for them, the number of expected fledglings cannot be greater than the number of adults that survive the incubation period divided by the parameter ***adminAdultsPerChick***. The standard value of this parameter is 0.5, under the assumption that if one parent dies, the remaining one can support two chicks.  $E_N$  is calculated as:

$$E_N = \min \left[ N_A (S_A)^{T_{LF}} / A, \sum (N_E (S_N)^{T_N}) (S_C)^{T_{CP}} \right]$$

where  $A$  is ***adminAdultsPerChick***, the summation is over all current nests,  $N_E$  is the number of viable eggs in the nest,  $T_N$  is the number of days left for the nest to incubate, and  $T_{CP}$  is the duration of the chick period (the parameter ***chickPeriodDurationMean***).



The expected number of fledglings from current chicks ( $E_C$ ) is modeled as the number of chicks now alive at the site times the rate of chick survival through the remaining chick period. Since chicks require adults to care for them, the number of expected fledglings cannot be greater than the number of adults that survive to the end of the chick period divided by the parameter ***adminAdultsPerChick***.  $E_C$  is calculated as:

$$E_C = \min \left[ N_A (S_A)^{T_{LF}} / A, \sum \left( (S_C)^{T_C} \right) \right]$$

where the summation is over all current chicks and  $T_C$  is the number of days left in the chick period.

The total number  $E_S$  of expected fledglings if adults stay at the site is then  $E_{UF} + E_N + E_C$ . The site is abandoned if  $E_S$  is less than the number of fledglings expected if the adults abandon the site ( $E_A$ ). The value of  $E_A$  is assumed to vary with the number of female adults currently alive, but also to decrease with time as the breeding season progresses. As the season progresses, it is assumed the expected reproductive output of females decreases due to factors such as reduced fecundity, lower energy reserves, and less time for re-nesting in case of nest and chick mortality. Expected reproduction reaches zero when there is no longer sufficient time for nests to incubate and chicks to fledge before the fall migration. It is assumed that the expected number of fledglings per female is ***adminExpectedFledges*** at the start of the nesting season and decreases linearly to zero at the date at which new nests can no longer be successful ( $T_{LN}$ , equal to ***manareaLastFledgingDate*** minus ***chickPeriodDurationMean*** minus ***nestIncubationDurationMean***).  $E_A$  is modeled as:

$$E_A = N_F R \left( \frac{(T_{LN} - T)}{(T_{LN} - T_{FA})} \right)$$

where  $N_F$  is the total number of female adults,  $T$  is the current date and  $T_{FA}$  is the date on which terns can first start arriving (parameter ***manareaFirstNestDate*** minus ***adultMinDaysArrivalToEggLaying***; Section 8.2).

To eliminate ambiguity, it is assumed sites cannot be abandoned when there are no adult females, nests, or chicks present (i.e., they are occupied only by male adults). The site abandonment submodel can be turned off by

setting the parameter ***adminExpectedFledges*** to zero. A negative value of this parameter can cause extreme site abandonment.

## 8.12 Random number generation

The random numbers used in the model are generated using *Repast's* random distributions, which are from the Colt library of scientific Java classes. The pseudorandom number generator driving the distributions uses the Mersenne Twister (MT19937) algorithm. The generator is seeded via model parameter ***adminSetRandomSeed***: if this parameter is 0 then the generator is seeded randomly (so its results are unique and not reproducible), but if the parameter has a positive integer value, that value is used to seed the generator (so the generator will produce the same sequence of pseudorandom numbers each time the model is executed).

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## Appendix A: Standard Parameter Values

The ILT model’s parameters, and their standard values, are summarized in this table. Parameters are organized by the type of model entity (Section 3) they are used by. Parameters not specific to one entity are referred to as “administrative.” Mortality agent parameters are presented in Appendix B.

Parameter (by entity)	Default Value
Adult	
<i>adultSiteSelectionDistance</i>	10,000
<i>adultSiteSelectionWaitDays</i>	10
<i>adultNestQualityRange</i>	0.2
<i>adultMinDaysArrivalToEggLaying</i>	14
<i>adultMaxNumBreedingAttempts</i>	2
<i>adultMinRenestingInterval</i>	5
<i>adultClutchProb1Egg</i>	0.1
<i>adultClutchProb2Eggs</i>	0.42
<i>adultFracNonviableEggs</i>	0.06
<i>adultMinNestArea</i>	37
Chick	
<i>chickPeriodDurationMean</i>	20
<i>chickPeriodDurationSD</i>	1.0
Nest	
<i>nestIncubationDurationMean</i>	21
<i>nestIncubationDurationSD</i>	1.5
Management Area	
<i>manareaFirstNestDate</i>	142 <sup>1</sup>
<i>manareaFracDispersers</i>	0.15
<i>manareaLastFledgingDate</i>	242 <sup>2</sup>

<sup>1</sup> Average of 29 site/year combinations for the Missouri, Platte, Niobrara, Arkansas, Mississippi, and Canadian rivers from the following 10 data sources: USACE (2011), Szell and Woodrey (2003), Kirsch (1990), Urbanic (2003), Leslie et al. (2000), Schwalbach et al. (1998), Smith and Renken (1990), Jenniges and Plettner (2008), Adolph et al. (2001), Byre (2000). Dates did not vary by latitude.

<sup>2</sup> Calculated by adding 41 days to the average last nesting date.

Parameter (by entity)	Default Value
<i>manareaLastNestDate</i>	201 <sup>1</sup>
<i>manareaNumAdults</i>	446
<i>manareaPeakNestDate</i>	155 <sup>2</sup>
<i>manareaSiteCodes</i>	(This parameter is a character string naming all the sites to include in a run; following is an example.) ARM465_7, ARM469_0, ARM470_0, ARM471_0, ARM473_5, ARM478_4, ARM478_5, ARM479_0, ARM479_2, ARM480_9, ARM481_0, ARM484_6, ARM486_0, ARM488_4, ARM488_8, ARM489_8, ARM492_4, ARM497_0, ARM509_0, ARM523_4, ARM475_7, ARM507_0
Admin	
<i>adminAbandSurvivalHorizon</i>	5
<i>adminAdultsPerChick</i>	0.5
<i>adminDisplayMediumQualityLowerThresh</i>	0.06561
<i>adminDisplayHighQualityLowerThresh</i>	0.59
<i>adminExpectedFledges</i>	1.0
<i>adminQualDist2Bank01</i>	100
<i>adminQualDist2Bank09</i>	400
<i>adminQualDist2ForestEdge01</i>	400
<i>adminQualDist2ForestEdge09</i>	600
<i>adminQualDist2Veg01</i>	50
<i>adminQualDist2Veg09</i>	500
<i>adminQualFreeboard01</i>	0.5
<i>adminQualFreeboard09</i>	1
<i>adminQualFreeboardAtMinSuitableFlow01</i>	1
<i>adminQualFreeboardAtMinSuitableFlow09</i>	3
<i>adminSetRandomSeed</i>	30609

<sup>1</sup> Average of 23 site/year combinations for the Missouri, Mississippi, Platte, Niobrara, and Arkansas Rivers from the following 8 data sources: USACE (2011), Szell and Woodrey (2003), Kirsch (1990), Urbanic (2003), Schwalbach et al. (1998), Smith and Renken (1990), Jenniges and Plettner (2008), and Adolph et al. (2001). Dates did not vary by latitude.

<sup>2</sup> Average of 16 site/year combinations for the Missouri, Platte, Niobrara, and Arkansas Rivers from the following 6 data sources: USACE (2011), Kirsch (1990), Urbanic (2003), Schwalbach et al. (1998), Jenniges and Plettner (2008), and Adolph et al. (2001). Dates did not vary by latitude.

## Appendix B: Example Mortality Agent Input

The mortality agent types and parameter values in this table were established as standard values prior to calibration of the model. Parameter names starting with “mam” are input as part of the database table that defines which mortality agent types exist; parameters with names starting with “magent” are set in the model’s parameter configuration file and hence can be changed without altering the database.

Parameter (by mortality agent type)	Default Value
Nest predator (e.g., coyote)	
<i>mamName</i>	NestPred
<i>mamMaxDiscoverRate</i>	0.022
<i>mamDuration</i>	7
<i>mamAdultsKilled</i>	0
<i>mamNestsKilled</i>	5
<i>mamChicksKilled</i>	0
<i>magentNestPred</i>	3.0 or 8.0 <sup>1</sup>
Chick predator (e.g., owl)	
<i>mamName</i>	ChickPred
<i>mamMaxDiscoverRate</i>	0.043
<i>mamDuration</i>	10
<i>mamAdultsKilled</i>	0
<i>mamNestsKilled</i>	0
<i>mamChicksKilled</i>	8
<i>magentChickPred</i>	3.0 or 8.0 <sup>2</sup>
Adult predator (e.g., falcon)	
<i>mamName</i>	AdultPred
<i>mamMaxDiscoverRate</i>	0.0003
<i>mamDuration</i>	10

<sup>1</sup> 3.0 is the default for the 2008-excellent conditions habitat input set. 8.0 is the default for the 2006-degraded conditions habitat input set.

<sup>2</sup> Same as above.

Parameter (by mortality agent type)	Default Value
<i>mamAdultsKilled</i>	2
<i>mamNestsKilled</i>	0
<i>mamChicksKilled</i>	0
<i>magentAdultPred</i>	3.0 or 8.0 <sup>1</sup>
Off-road vehicles	
<i>mamName</i>	ORV
<i>mamMaxDiscoverRate</i>	0.028
<i>mamDuration</i>	3
<i>mamAdultsKilled</i>	0
<i>mamNestsKilled</i>	0.5
<i>mamChicksKilled</i>	0.25
<i>magentORV</i>	3.0

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<sup>1</sup> Same as above.



## Appendix C: Output Summary Statistics

This appendix describes one kind of observation of the ILT model produced by its software (Section 5.8). For each model run, summary metrics are calculated at the end of the simulated breeding season to characterize how successful tern reproduction was and which factors affected success or failure. These summary statistics are reported for each site, reach, and management area and logged to the model database's (**tblResults**) table. Many different metrics are reported so that model results can be compared to many different field studies, which use a variety of metrics.

Since adult terns can move between sites, reporting statistics about them according to site requires a convention that specifies which adults belong to which site. The convention used for these outputs is that an adult is assigned to the last site it occupied before being removed from the model because it succeeded or failed at breeding or was killed. Any adults that are initialized but fail to select a site would not appear in these statistics. The following table lists and describes the summary metrics.

Summary statistic	Description
Number of adults	Total number of adults
Number of females	Number of adults with sex = female
Number of nests	Total number of nests created
Number of successful nests	Count of nests with number of hatched eggs $\geq 1$ (such nests are also referred to here as "broods")
Number of chicks	Total number of hatched eggs
Number of fledglings	Number of fledging events
Hatching success	Number of hatched eggs / number of eggs
Nest success	Number of successful nests / number of nests
Fledging success	Number of fledglings / number of hatched eggs
Proportion of breeding adults	The number of adults with <i>adtBreedingAttempt</i> > 0 / number of adults (only calculated at scale of management area)
Reproductive success	Number of fledglings / number of females (can only be calculated at scale of management area)
Mean chicks per nest	Number of hatched eggs / number of nests
Mean fledglings per nest	Number of fledglings / number of nests

Summary statistic	Description
Mean clutch size	Number of eggs / number of nests
Number of 1, 2, and 3-egg clutches	Three statistics: Number of nests with 1 egg (whether viable or not); number of nests with 2 eggs; number of nests with 3 eggs
Number of females with 0, 1, 2, or 3 breeding attempts	Number of females with <i>adtBreedingAttempt</i> = 0, 1, 2, or 3
Number of nests destroyed by all possible mortality types	Multiple statistics: Number of nests destroyed by each mortality type (see sections 4.9 and 4.10 and Table 5.8 for list of mortality types)
Number of chicks destroyed by all possible mortality types	Multiple statistics: Number of chicks destroyed by each mortality type
Number of adults destroyed by all possible mortality types	Multiple statistics: Number of adults destroyed by each mortality type

# REPORT DOCUMENTATION PAGE

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<b>13. SUPPLEMENTARY NOTES</b>					
<b>14. ABSTRACT</b> TernCOLONY is an individual-based model of Least Tern reproduction. The model simulates the reproduction of all individuals within virtual Least Tern breeding populations on large rivers below multi-purpose dams. Breeding seasons are simulated in daily time steps. Users may specify different habitat inputs, representing excellent and degraded nesting habitat conditions. After choosing baseline habitat conditions for simulations, users may choose to add "restoration" sandbars to simulations to understand how different scenarios of habitat creation may affect regional reproduction. In addition to specifying habitat conditions, users may specify a range of daily flow inputs (simulating reservoir operations during wet years, dry years, or years with mid-season floods). Users may also specify a range of predator and human disturbance intensities or initial tern population sizes. By repetitively simulating different scenarios of initial conditions, users may learn if and how different factors limit regional Least Tern reproduction or how alternative management strategies may perform to increase reproduction. This document, the model description, is the first in a series of publications that describe the TernCOLONY model. The TernCOLONY model description follows the "ODD" (Objectives, Design Concepts, and Details) protocol of Grimm et al. (2006) as updated by Grimm et al. (2010) for describing individual-based models. This protocol starts with general and conceptual characteristics (sections 2-5); followed by the detail needed to make the model reproducible (sections 6-8). Full context for the model development, testing, and analysis process is given in Lott et al. (2012a), which also contains sections describing major model inputs (e.g., habitat and flow datasets) for specific study sites. Most users will access TernCOLONY via the web-based graphical user interface located at <a href="http://www.leasttern.org">http://www.leasttern.org</a> . The model description provides the foundation upon which all subsequent publications related to TernCOLONY will rely.					
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