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Temporal Dynamics of Galapagos Marine Iguna (Amblyhynchus Cristatus) Haulout

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ABSTRACT

TEMPORAL DYANAMICS OF GALÁPAGOS MARINE IGUANA

(*AMBLYRHYNCHUS CRISTATUS*) HAULOUT

by

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ABSTRACT OF GRADUATE STUDENT RESEARCH

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Title: TEMPORAL DYNAMICS OF GALÁPAGOS MARINE IGUANA (*AMBLYRHYNCHUS CRISTATUS*) HAULOUT

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Galápagos marine iguanas (*Amblyrhynchus cristatus*) briefly forage in marine habitats but spend their remaining time hauled out on land. A wide range of diurnal activities, from social and thermoregulatory behaviors to sleep and food processing, occurs during haulout. To understand the dynamics of haulout and foraging in relation to environmental factors, I fit compartmental models derived from ordinary differential equations to field data collected daily from 30 April to 16 May 2011 at two sites—one Sandy and one Rocky—at Cabo Douglas, Isla Fernandina. The best model for haulout at the Sandy site accounts for 77–80% of observed variability and includes the environmental variables solar elevation, heat index, tide height, and relative humidity. Using only the predictable variables of solar elevation and tide height, the model still

accounts for 72% of system variability. The best model for haulout at the Rocky site includes solar elevation, THW index, tide height, and hour of day, and accounts for 57% of observed variability. Using only solar elevation, tide height, and hour of day, the model still accounts for 51% of the variability. Poisson regression supports these results with few inconsistencies and provides further insight into system dynamics. Although the environmental variables that predict haulout are different across sites, the methodology is powerful and could benefit conservation measures developed for this endemic species.

Andrews University

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TEMPORAL DYANAMICS OF GALÁPAGOS MARINE IGUANA

(*AMBLYRHYNCHUS CRISTATUS*) HAULOUT

A Thesis

Presented in Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

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To my parents,
who have taught me to wonder;
may I always be your peace dancing.

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CHAPTER I

INTRODUCTION

Since their first description in the early 1800s, Galápagos marine iguanas (*Amblyrhyncus cristatus*) have attracted attention from the scientific community (Bell, 1826; 1843). Although they spend the majority of time hauled out on land, they are the only lizards that feed exclusively in marine habitats (Darwin, 1839; White, 1973; Trillmich and Trillmich, 1986). Because their survival could be threatened without strict conservation measures, marine iguanas are protected under an international agreement (Secretariat, 2011).

Previous studies of marine iguanas have examined the physiology supporting their unique lifestyle. Physiological attributes underlying thermoregulatory behaviors, osmoregulation, and metabolic costs of locomotion have been particularly well studied (Dunson, 1969; Bennett and Dawson, 1975; Bartholomew et al., 1976; Gleeson, 1979; Gleeson, 1980; Nagy and Shoemaker, 1984; Shoemaker and Nagy, 1984). The ecology, behavior, and population dynamics of marine iguanas during El Niño events and other stressful occasions also have received attention (Kruuk and Snell, 1981; Laurie, 1990; Laurie and Brown, 1990a; Laurie and Brown, 1990b; Wikelski and Thom, 2000; Romero and Wikelski, 2001; Vinueza et al., 2006). Statistical trends in foraging commonly are reported in these studies. Haulout, the converse of foraging, incorporates both periods of rewarming at non-colony locations between brief foraging bouts and final landing at colony locations in the evening (Nagy and Shoemaker, 1984; Trillmich and Trillmich, 1986; Wikelski et al., 1993; Wikelski and Trillmich, 1994). A wide spectrum of activities including social interactions, sleep, thermoregulatory behaviors, and food processing is encompassed in haulout.

Factors involved in foraging behavior and haulout also have been explored. For example, body size determines whether iguanas forage in subtidal or intertidal zones, with smaller iguanas foraging exclusively in the intertidal zone around low tide, larger iguanas more likely foraging in the subtidal zone, and the largest individuals foraging exclusively in the subtidal zone (Trillmich and Trillmich, 1986; Buttemer and Dawson, 1993; Wikelski and Trillmich, 1994). Because intertidal feeders are likely to forage near low tide, tide height conceivably plays a role in the dynamics of haulout by these animals. The ectothermic physiology of marine iguanas makes them particularly sensitive to the dramatic temperature differences between the terrestrial (up to 60ºC) and marine environments (14–25ºC) they occupy (White, 1973; Bennett and Dawson, 1975; Dawson et al., 1977). Because food processing, metabolic recovery from intense activity, and possibly osmoregulation are all thermolabile processes, time of day and ambient temperature have been postulated as factors affecting haulout (Dunson, 1969; Gleeson, 1980; Buttemer and Dawson, 1993; Wikelski and Trillmich, 1994; Fields et al., 2008).

Although previous studies highlighted the effects of environmental variables on temporal patterns of haulout in marine iguanas, no study has incorporated these abiotic variables into an integrated model. In recent years, compartmental differential equation models connected rigorously to field data have accurately described, explained, and predicted loafing in marine birds and haulout in marine mammals as functions of environmental cues (Henson et al., 2004; Hayward et al., 2005; Henson and Hayward, 2010). Marine iguanas, like marine birds and mammals, have a terrestrial yet partially aquatic lifestyle, exhibit haulout behaviors, and tend to assemble in large terrestrial aggregations. This suggests the possibility of modeling their haulout behavior with similar techniques (Carpenter, 1966; White, 1973; Wikelski et al., 1996; Wikelski, 1999).

In this study I apply the differential equation techniques, as well as Poisson regression, to determine which environmental variables are associated with marine iguana haulout. Specifically, I (1) test the null hypothesis that temporal haulout patterns of marine iguanas are independent of tide height, solar elevation, and meteorological variables, and (2) compare a suite of alternative hypotheses (models) that include these factors. The models provide a quantitative tool with which managers can predict future daily haulout and track long-term trends in population size.

CHAPTER II

METHODOLOGY

Data Collection

Field data were collected at Cabo Douglas, Isla Fernandina, Galápagos, between 30 April and 16 May 2011. I selected two study sites, a primary Sandy site and a secondary Rocky site. The Sandy site (0º18'16 S, 91º39'06 W, Google Earth; 425 m^2) consisted of a sandy beach opening into a shallow embayment known as "Sea Lion Bay" (Fig. 1). It was bordered by rocks on the sides and a dense stand of salt bush (*Cryptocarpus pyriformis*) in the back. The Rocky site (0º18'11 S, 91º39'09 W, Google Earth; 65 m^2) consisted of a relatively flat-topped lava outcrop bordering the open sea. It extended above the upper intertidal zone and was easily viewed from a high basaltic outcrop that sheltered the west side of Sea Lion Bay (Fig. 2). Hundreds of iguanas hauled out at each site daily.

I analyzed iguana haulout as a function of environmental variables using mathematical modeling and Poisson regression. Data consisted of haulout censuses and haulout flux counts taken during 10- and 30-min intervals and environmental variables logged every 0.5 hr. The data collection methodology for each site differed and is detailed as follows.

Iguana Flux and Haulout Data

Sandy Site Fluxes

Given the tendency of hauled-out iguanas to pile on top of one another, it was not feasible to conduct accurate repeated census at time intervals small enough to capture the main dynamics of the system. In contrast, it was possible to count the number of iguanas entering and exiting the beach during small time intervals. I therefore conducted one census each day near noon when few animals were present, and during the rest of the day I counted influx and efflux rates across the beach–water interface.

From an observation point approximately 50 m from the Sandy site, I tallied all animals entering or leaving the water during set time intervals as follows: From 30 April–7 May fluxes were tallied during 06:00–18:00 local standard time (LST), and from 8 May–16 May they were tallied during 07:00–17:30 LST because iguanas moved little before and after these times. From 30 April–4 May I counted fluxes at 30-min intervals. I noted, however, that 30-min intervals were too long to capture the dynamics of the system. Thus, from 5 May–16 May, during the time of day when the majority of site activity occurred (typically 08:30–15:30), I counted fluxes at 10-min intervals; before and after that time I reverted to 30-min intervals. Ten-minute time intervals began each day at variable times, before the first iguana exited the study site but after the majority of iguanas at the site had assumed elevated basking postures and oriented parallel to incident radiation.

All data collected were used in the mathematical models, regardless of daily start time or length of time interval. For Poisson regression analysis, all flux data were converted to 30-min intervals.

Let N_c denote a census at the Sandy site. The extrapolated occupancy at the beginning of the next time interval, given that *x* iguanas left the site to enter the water and *y* iguanas exited the water to haul out during that interval, was computed to be

$$N_{c+1} = N_c - x + y.$$

Similarly, at the beginning of the time interval just prior to the census, given that *x* iguanas left the site and *y* iguanas hauled out during that interval, the inferred occupancy was

$$N_{c-1} = N_c + x - y.$$

In this way inferred occupancies were extrapolated forward to the end of the day and backward to the beginning of the day, creating a times series of inferred occupancies for each day.

Iguanas regularly entered into and exited the salt bush surrounding the Sandy site. As far as I could determine, the animals did not use alternate exits to the sea from the salt bush, but once in the salt bush they could not be counted. Thus, N_c was sometimes artificially low. This resulted in two problems: (1) inferred occupancy could yield negative numbers of iguanas, and (2) inferred occupancies for evenings and ensuing mornings sometimes were mismatched.

For each day with negative inferred occupancies (Table A- 1), I subtracted the most negative inferred occupancy from the census and from each inferred occupancy for that day. That is, I added the absolute value of the most negative inferred occupancy to each occupancy for that day. This set the minimal inferred occupancy to zero by adding in any iguanas within the salt bush that day which chose to exit the site. (This did not always solve the mismatched overnight occupancy problem; see Discussion.)

Stratified random sampling techniques were used to divide the inferred occupancies for the Sandy site into two sets: an estimation data set for model parameterization and a validation data set for model validation. I divided the 14-day tidal cycle into 4 segments of 3.5 days and binned the inferred occupancies. I randomly assigned a value of 0 or 1 to each inferred occupancy, then for each bin randomly designated 0's or 1's as the subset for model validation (Table A- 2).

Rocky Site Haulout

From 30 April–16 May 2011 I digitally photographed Rocky site occupants at 30-min intervals from a vantage point approximately 40-m distant from the Rocky site. Photographs were taken during 06:00–18:00 through 7 May; after 7 May they were taken during 07:00–17:30, for a total of 398 photographs.

Seventeen photographs were lost due to file corruption or technology failures (Table A- 3). I excluded another 19 photographs due to abnormal haulout patterns caused by high tide coupled with winds of 29 ms^{-1} from the SSW. In particular, when high tide occurred in midafternoon on 6 May with waves intermittently flooding the site, starting at 15:00 iguanas left the Rocky site for higher ground. Because iguanas are inactive at night, the perturbation in haulout persisted until iguanas began returning to the site for haulout at 13:00 the following day (Nagy and Shoemaker, 1984; Buttemer and Dawson, 1993).

In each of the remaining 362 photographs, iguanas were marked and counted. The resulting data set consisted of daily time series of iguana occupancies at 30-min intervals (Table A- 2).

Environmental Data

Meteorological data were logged every 30 min by a Davis VantageVue™ weather station located 1.8 m above site elevation on a white sand beach located between the Sandy site and the Rocky site. Data logged included temperature, humidity, dew point, wind speed, wind direction, wind chill, heat index, THW index (a measure of ambient conditions based on temperature, humidity, and wind speed), and barometric pressure (Table 1).

Tide heights (in m) were determined every 30 min during hours of iguana observation using a vertical 4-m surveyor pole on the western side of Sea Lion Bay, south of the high basaltic outcrop. This area usually was protected from the surf. Solar flux (Wm^{-2}) was obtained by a hand-held TM-206 Solar Power Meter (Ambient Weather) that was recalibrated before each sampling event. Solar elevations (in degrees above the horizon) were obtained from a National Oceanic and Atmospheric Association (NOAA) online calculator (http://www.srrb.noaa.gov/highlights/sunrise/azel.html). Seawater temperature data were obtained from a HOBO Temp Pro located at the point of Cape Douglas (0º18'06" S 91º39'10"W) at 10-m depth relative to the sea surface at time of deployment (courtesy of the Charles Darwin Foundation and Godfrey Merlen). Data are shown in Table A- 4.

I translated wind direction to a circular scale with 0º and 360º at true North and then transformed to a linear scale according to:

$$D_{linear} = \left\{ \begin{array}{ccc} D_{circular} & if & D_{circular} \leq 180 \\ 360 - D_{circular} & if & D_{circular} \geq 180 \end{array} \right\}.$$

To interpolate tidal values for the 10-min time intervals, I fit a smooth curve through the tide height data using the Lowess smoothing function in Axum 5.0 (Mathsoft Inc., Cambridge, MA; [10 iterations, 25% points for each local regression, 100 output points]). Using Matlab R2011b (Mathworks, Natick, MA; http://www.mathworks.com) I then splined the output and obtained tide heights for each time at which iguana occupancy was inferred. Values for solar elevation at 30- and 10-min time intervals were obtained in the same manner as those for tide height. For the other environmental variables, I interpolated 10-min time interval values linearly using the surrounding values. I did not smooth these variables as I did with the tidal and solar elevation data due to the greater variability in values around the daily trend.

All environmental variables were then nondimensionalized and scaled so that their values always occurred between 1 and 2 (Damania et al., 2005; Henson et al., 2007a; Henson et al., 2007b; Moore et al., 2008). This was accomplished by subtracting the minimum value, dividing by the new maximum value, and then adding 1. For example, to nondimensionalize and scale some variable *S*:

$$S_{scaled} = \frac{S_{unscaled} - \min(S_{unscaled})}{\max\left(S_{unscaled} - \min(S_{unscaled})\right)} + 1.$$

Mathematical Model

Deterministic Model

The deterministic model is based on assumptions similar to those found in related studies (Hayward et al., 2009; Cowles, 2011).

(1) The number of iguanas hauled out at the study site can be described by a two-compartment model consisting of (a) the study site and (b) all places other than

the study site.

(2) Fluctuations in numbers of iguanas at the study site were density-independent and occurred in direct response to environmental variables that varied in time *t*. Specifically, iguanas arrived at the site at a per capita rate proportional to a function $E_{12}(t)$ of environmental variables and left the site at a per capita rate proportional to a function $E_{21}(t)$ of environmental variables, independent of the number of iguanas in either compartment.

(3) The rate functions $E_{12}(t)$ and $E_{21}(t)$ are multiplicative functions of powers of environmental variables (Damania et al., 2005; Henson et al., 2007a; Henson et al., 2007b; Moore et al., 2008). This is analogous to the assumption required for log-linear (Poisson) regression of the fluxes on the environmental factors (Mccullagh and Nelder, 1989).

(4) (a) The maximum number of iguanas eligible to haul out at the Sandy site during the study was proportional to

$$Q(t) = \eta + \delta \sin(\gamma(\text{day of year} + t/24)) \quad , \qquad (1a)$$

where *t* is the hour of day and $\eta, \delta, \gamma > 0$ are constant parameters estimated from daily maximum inferred occupancies. Tidal fluctuations appeared to circumscribe maximal haulout, making the sine wave a reasonable approximation for the functional form.

(b) The maximum number of iguanas eligible to haul out at the Rocky site during the study was proportional to

$$Q(t) = S_e^{\iota}(t) \quad , \qquad (1b)$$

where $S_e(t)$ is the solar elevation at time *t* and $\iota > 0$ is a parameter to be estimated from Rocky site haulout data. This assumption is motivated by the fact that haulout at the Rocky site experienced daily downturns at low solar elevations because iguanas moved out of the sample area to nearby rocks.

(5) The system can be decomposed into two timescales, a slow time scale that describes steady state dynamics, and a fast time scale that describes recovery from disturbance (Hoppensteadt, 1974; Henson et al., 2006). Note, however, that no disturbances were observed in this study.

Based on the first assumption, I used a two-compartment ordinary differential equation model. Let $N(t)$ represent the number of animals occupying a study site at time t. The net rate of change of the number N of animals at the site is the difference between the rate at which iguanas arrive at the site and the rate at which they leave:

$$\frac{dN}{dt} = [\text{inflow}] - [\text{outflow}]. \tag{2}$$

Let $M(t)$ represent the total number of iguanas in the two-compartment system at time t. From assumption two, the per capita inflow rate is $E_{12}(t)$ multiplied by a constant of proportionality $a > 0$. The total inflow rate is therefore $aE_{12}(t)(M(t) - N(t))$, where $M(t) - N(t)$ is the number of animals that may haul out at the site but have not done so. Similarly, the total outflow rate is $bE_{21}(t)N(t)$. Substituting these into (2) yields

$$\frac{dN}{dt} = \left[aE_{12}(t)\big(M(t) - N(t)\big)\right] - \left[bE_{21}(t)N(t)\right] . \tag{3}$$

The dynamics of (3) occur on two time-scales, given assumption five. The undisturbed "steady state" dynamics of the system are well approximated by the algebraic equation

$$0 = aE_{12}(t)\big(M(t) - N(t)\big) - bE_{21}(t)N(t) \tag{4}$$

(Hoppensteadt, 1974; Henson et al., 2006). Solving for $N(t)$ yields

$$N(t) = \frac{M(t)}{1 + \frac{bE_{21}(t)}{aE_{12}(t)}} \ . \tag{5}$$

Defining $\alpha = b/a$ and $E(t) = E_{21}(t)/E_{12}(t)$ and noting that (by assumption four) $M(t)$ is proportional to the functional forms in (1a) and (1b) yields deterministic models for the Sandy site

$$N(t) = \frac{\beta\left(\eta + \delta \sin(\gamma(\text{day of year} + t/24))\right)}{1 + \alpha E(t)} \tag{6a}$$

and for the Rocky site

$$N(t) = \frac{\beta S_e^{\iota}}{1 + \alpha E(t)} \ . \tag{6b}$$

By assumption three, $E(t)$ is a multiplicative function of powers of environmental variables. In model (6a) parameters $\gamma, \delta, \eta > 0$ are estimated from daily maximum inferred occupancies at the Sandy site, and $\alpha, \beta > 0$ are parameters to be estimated from the time series of inferred occupancies. In model (6b) $\alpha, \beta, \iota > 0$ are parameters to be estimated from Rocky site haulout counts.

Stochastic Model

Deterministic models are approximations of real systems that capture the main trends in data. Because ecological systems are complex, model predictions are expected to deviate from data. The difference between an observed value and the associated predicted value is called a residual. Residuals can be viewed as realizations of a random variable having some hypothesized distribution. Stochastic models provide assumptions regarding the distribution of residuals and therefore form the basis for parameter estimation.

Process noise generally falls into one of two categories: (1) environmental stochasticity, in which extrinsic events experienced by all individuals in a population cause variability over time and (2) demographic stochasticity, which arises from individual variability in intrinsic parameters (Cushing et al., 2003; Henson et al., 2007a). Environmental stochasticity is approximately additive on the logarithmic scale, whereas demographic stochasticity is approximately additive on the square-root scale (Dennis et al., 2001; Cushing et al., 2003).

I assumed environmental stochasticity was the dominant type of noise associated with model (1a); although tidal fluctuations deterministically imposed a maximum haulout envelope on the system, other environmental forces such as wave height caused deviations from model predictions. The stochastic version of model (1a) is therefore

$$\ln\left(Q(t)\right) = \ln\left(\eta + \delta \sin(\gamma(\text{day of year} + t/24))\right) + \sigma\varepsilon(t), \qquad (8)$$

or equivalently,

$$Q(t) = \left(\eta + \delta \sin(\gamma(\text{day of year} + t/24))\right)e^{\sigma\varepsilon(t)}, \qquad (9)$$

where $\varepsilon(t)$ are standard normal random variables uncorrelated in time and $\sigma > 0$ is a constant parameter representing standard deviation. Because model (1b) did not require parameterization separately from (6b), no stochastic version of this model was created.

I assumed that demographic stochasticity was the dominant type of noise associated with models (6a) and (6b), given that all major environmental correlates were incorporated explicitly into the models. In this context, demographic stochasticity arises from independent, random, binary choices of individual iguanas as they arrived at or departed from the study site. The stochastic version of model (6a) is

$$\sqrt{N(t)} = \sqrt{\frac{\beta\left(\eta + \delta \sin(\gamma(\text{day of year} + t/24))\right)}{1 + \alpha E(t)}} + \sigma\varepsilon(t), \qquad (10)$$

or equivalently,

$$N(t) = \left(\sqrt{\frac{\beta\left(\eta + \delta \sin(\gamma(\text{day of year} + t/24))\right)}{1 + \alpha E(t)}} + \sigma\varepsilon(t)\right)^2 . \qquad (11a)$$

Similarly, the stochastic version of model (6b) is

$$N(t) = \left(\sqrt{\frac{\beta S_e^{\iota}}{1 + \alpha E(t)}} + \sigma\varepsilon(t)\right)^2 . \qquad (11b)$$

In (11a) and (11b), the righthand side is taken to be zero if the quantity inside the parentheses is negative.

Model Parameterization

Parameters were estimated by maximum likelihood techniques using the nonlinear least squares (LS) method, which minimizes the residual sum of squares

$$RSS(\theta) = \sum_{data}\left(f(\text{observation}) - f(\text{prediction})\right)^2$$

as a function of the vector θ of model parameters. Here $f(x) = \ln(x)$ or $\sqrt{(x)}$, depending on the type of stochasticity. The minimizer $\hat{\theta}$ represents the LS parameter estimates. I generated the model predictions using Matlab R2011b (Mathworks, Natick, MA; http://www.mathworks.com) and minimized $RSS(\theta)$ using the Matlab function fminsearch.

I obtained parameters for sub-model (1a) by fitting it to *maximal* daily inferred occupancies of the complete Sandy site data set. I then estimated the remaining parameters in model (6a) by fitting it to the estimation data set of inferred occupancies for the Sandy site. The parameters in model (6b) were estimated by fitting it to the complete set of Rocky site occupancies.

Model Selection

By assumption three,

$$E(t) = X_1^{\Omega_1} X_2^{\Omega_2} \ldots X_{14}^{\Omega_{14}},$$

where the X_i are the 14 environmental variables monitored at the site (Table 1) and the Ω_i are constant parameters that can be positive, zero, or negative. Estimation of 16 or 17 parameters (14 exponents plus the coefficients α, β, and ι) was intractable. I therefore posed a suite of alternative models by using various subsets of the 14 environmental variables and used theoretic information theory to select the best model for each site.

Over 16,000 unique models can be generated for each site with 14 different environmental variables. I used the following method to limit the number of alternatives:

(1) I graphically analyzed environmental variables for covariance and calculated coefficients of correlation. I did not include highly correlated variables ($r > 0.8$) or collinear ($r > 0.89$) in the same model.

(2) I tried each environmental variable by itself in the numerator and the denominator of the environmental function $E(t)$ (that is, I tried it with $\Omega_i > 0$ and $\Omega_i < 0$). For cases in which Ω_i would not parameterize, I forced it to be of integer value.

(3) I created increasingly complex models through step-wise combinations of environmental variables—that is, two-variable combinations, then three-variable combinations, and so on. Variables whose addition did not further minimize the RSS after parameterization were discarded after each step.

This process created 155 alternative models for the Sandy site and 44 for the Rocky site. To determine the best model for each site, I used the Akaike Information Criterion (AIC), which penalizes models with more parameters for over-fitting. In the case of LS methodology, the criterion is equivalent to

$$\mathrm{AIC} = n \ln \hat{\sigma}^2 + 2\kappa ,$$

where n is the number of observations, $\hat{\sigma}^2 = \mathrm{RSS}(\hat{\theta})/ n$ is the variance of the likelihood function as estimated from the minimized residuals, and κ is the number of model parameters, including $\hat{\sigma}^2$ (Burnham and Anderson, 2002). The model with the lowest AIC value, $\mathrm{AIC}_{\min}$, is considered the best model. Models are ranked according to $\Delta_i = \mathrm{AIC}_i - \mathrm{AIC}_{\min}$ with the best model having $\Delta_i = 0$. A model with $\Delta_i > 10$ is deemed significantly worse than the best model and can be omitted from consideration (Burnham and Anderson, 2002).

Goodness-of-Fit

Goodness-of-fit was calculated as

$$R^2 = 1 - \frac{RSS(\hat{\theta})}{\sum_{data} \left(f(\mathrm{data}) - \mathrm{mean}[f(\mathrm{data})] \right)^2} ,$$

where $RSS(\hat{\theta})$ is the minimized residual sum of squares and $f(x) = \ln(x)$ in the case of submodel (1a) and $f(x) = \sqrt{(x)}$ in the case of models (6a) and (6b). The R^2 value represents the proportion of variability explained by the model, with $R^2 = 1$ representing a perfect fit.

The best models ($\Delta_i = 0$) for the Sandy and Rocky sites were selected separately. The best model for the Sandy site was validated on the independent Sandy site validation data set without reparameterizing. It also was tested on the Rocky site data.

Regression Analysis

To quantify the individual effects that different environmental variables have on haulout (Table 1), I used Poisson regression, corrected for overdispersion, to analyze the Sandy site and Rocky site data as a function of 10 environmental variables: solar radiation, solar elevation, tide height, seawater temperature, ambient temperature, relative humidity, dew point, wind speed, wind direction and barometric pressure. I did not include wind chill, heat index, or THW index as regression factors because they were collinear ($r > 0.89$) with ambient temperature. The log-transformed dependent variable, when graphed against hour of day, showed a parabolic rather than linear trend; hence hour of day was not included as a regression factor. For the Sandy site, I regressed iguana influx and efflux separately on the environmental variables; for the Rocky site, I regressed haulout numbers (derived from the photographs) on the environmental variables.

To allow straightforward interpretation of the regression coefficients, the environmental variables were not nondimensionalized or scaled. Wind direction was translated to the (numeric) circular scale. Although this creates a discontinuity at true north, wind directions shifting across north–northeast and north–northwest rarely occurred (see trends of environmental variables in Results, also Table A- 4).

The Poisson regression coefficients are interpreted in the following way: For a one-unit change in a given environmental variable, the difference in the logs of expected counts is predicted to change by the respective regression coefficient, given that all other variables in the regression model are held constant. Positive regression coefficients indicate direct relationships and negative coefficients denote indirect relationships.

CHAPTER III

RESULTS

Trends in Environmental Variables

Descriptive statistics for the environmental variables appear in Table 2. Additionally, trends over the study period for all variables except tide height (see Mathematical Modeling below) are shown in Fig. 3. On an hourly basis, solar radiation was variable; cloud cover regularly changed insolation by hundreds of Wm^{-2} over short periods of time. The overall daily trend, however, matched that of solar elevation; values were low in the morning and increased to a midday maximum before decreasing through the afternoon to values near zero. Solar radiation and solar elevation were highly correlated ($r = 0.796$). Ambient temperature, wind chill, heat index, and THW index varied collinearly with each other ($r > 0.89$ for each correlation); daily trends matched those of solar elevation, although they were more variable. Dew point also exhibited a daily trend similar in shape to that of solar elevation but with increased variability, and averaged approximately 2º C cooler during the second half of the study period. The daily trend in relative humidity was roughly the inverse of solar elevation; it is lowest at midday and higher in the morning and evenings. The variability over the trend in relative humidity was comparable to that observed in ambient temperature, wind chill, heat index, and THW index.

Prevailing winds changed from easterly directions in the mornings to directions between south to west–southwest by late morning to mid-afternoon, although brief gusts from other directions occurred. Only on 11 May did prevailing winds shift back to easterly directions in the afternoon. Wind speed typically exhibited a daily pattern similar to that of solar elevation and averaged over 10 ms^{-1} higher in the afternoons than in the mornings. High winds (35–44 ms^{-1}) were predominantly from the southwest or south–southwest and occurred during nearly two thirds of all afternoons.

Tide was semi-diurnal with time of high tide shifting by approximately 50 min each day. Although there was a decreasing trend in seawater temperature over the course of the study, daily patterns in seawater temperature were highly variable, dependent on rainfall, solar radiation, and wind patterns. Seawater was approximately 3ºC cooler at the end of the study period than at the beginning, and averaged nearly 10% lower during the second half of the study period. Barometric pressure had a unique daily trend; values increased for a short period each morning, then fell through midmorning to later afternoon before increasing slightly each evening.

Mathematical Modeling

Sandy Site

Daily maximal haulouts at the Sandy site were highest around neap tide (10 May 2011, day of year 130, Fig. 4A), and lowest at spring tide (16 May, day of year 136, Fig. 4A). This motivated the choice of a sine wave as the functional form circumscribing maximal haulout at the Sandy site. Parameterization of this functional form, submodel (1a), yielded

$$Q(t) = 247.679 + 125.176\sin(0.448089(\text{day of year} + t/24)) \quad (12)$$

with $R^2 = 0.918$. The period of this sine wave (2π/0.448089) is just over 14 days, a complete tidal cycle. *Post hoc* analysis of the distribution of residuals is consistent with the assumption of environmental noise (Fig. 5).

Parameterization of model (6a) yielded 3 models with $\Delta_i < 1$ and approximately the same goodness-of-fit (Table 3). The best model ($\Delta_i = 0$, $R^2 = 0.7713$) has the environmental function

$$E(t) = \frac{S_e^{\varsigma} H_x^{\phi}}{H_u^{\psi} T^{\rho}}, \tag{13}$$

where S_e, H_x, H_u, and T represent solar elevation, heat index, relative humidity, and tide height, respectively (see Table 1 for all environmental variable abbreviations). The second best model ($\Delta_i = 0.3448$, $R^2 = 0.7711$) has the environmental function

$$E(t) = \frac{S_e^{\varsigma} T_x^{\omega}}{H_u^{\psi} T^{\rho}}, \tag{14}$$

where T_x represents THW index, and the third best model ($\Delta_i = 0.7241$, $R^2 = 0.7709$) has the environmental function

$$E(t) = \frac{S_e^{\varsigma} A^{\zeta}}{H_u^{\psi} T^{\rho}}, \tag{15}$$

where A represents ambient temperature. Alternative models with $\Delta_i < 10$ appear in Table 3.

Substituting (12) and (13) into (6a) with rounded LS parameter estimates yields

$$N(t) = \frac{\beta(247.7 + 125.2\sin(0.4481(\text{day of year} + t/24)))}{1 + \alpha\left(\frac{S_e^{\varsigma} H_x^{\phi}}{H_u^{\psi} T^{\rho}}\right)} \tag{16}$$

where β = 0.89595, α = 5.0812E-06, ς = 24.057, ϕ =1.8040, ψ = 6.7644, ρ = 2.4393, and each environmental variable is itself a function of time. *Post hoc* analyses revealed that the distribution of residuals is consistent with the assumption of demographic noise (Fig. 7A) but that the residuals are significantly auto-correlated (r = 0.95, p < 0.01). (See discussion.)

Fig. 6 shows model (16) predictions and inferred occupancies for the Sandy site, along with solar elevation and tide height. Model (16) indicates that the number of hauled-out iguanas decreases with increasing solar elevation and heat index and increases with increasing tide height and relative humidity.

The goodness-of-fit for model (16) on the independent validation data set (without reestimating LS parameters) was R^2 = 0.798, indicating successful model validation on the Sandy site. However, model (16) yielded a negative R^2 when tested on the Rocky site data without reparameterizing.

Rocky Site

Three Rocky site models had Δ_i < 10 (Table 3). The best model for the Rocky site (Δ_i = 0, R^2 = 0.5671) has environmental function

$$E(t) = \frac{S_e^{\varsigma} T_x^{\omega}}{H_r^{\xi} T^{\rho}} , \qquad (17)$$

where H_r represents the hour of day. The second best model (Δ_i = 0.4943, R^2 = 0.5665) has environmental function

$$E(t) = \frac{S_e^{\varsigma} H_x^{\phi}}{H_r^{\xi} T^{\rho}} , \qquad (18)$$

and the third model (Δ_i = 9.550, R^2 = 0.5556) has environmental function

$$E(t) = \frac{S_e^{\varsigma} W_c^{\varphi}}{H_r^{\xi} T^{\rho}}, \tag{19}$$

where W_c represents wind chill.

The fourth and fifth best Rocky site models had $\Delta_i > 10$, but are reported in Table 3 for comparison to Poisson regression analysis.

Substituting (17) into (6b) with LS parameter estimates yields

$$N(t) = \frac{\beta S_e^{\iota}}{1 + \alpha \left(\frac{S_e^{\varsigma} T_x^{\omega}}{H_r^{\xi} T^{\rho}} \right)} \tag{20}$$

where $\beta = 198.41$, $\iota = 0.94372$, $\alpha = 1.3513\text{E-}05$, $\varsigma = 17.857$, $\omega = 5.6945$, $\xi = 4.7029$, $\rho = 3.2322$, and each environmental variable is itself a function of time. *Post hoc* analyses revealed that the distribution of residuals is consistent with the assumption of demographic noise (Fig. 7B), but that the residuals are significantly auto-correlated ($r = 0.75$, $p < 0.01$). (See Discussion.)

Fig. 8 shows model (20) predictions and occupancies for the Rocky site, along with solar elevation and tide height. Model (20) indicates that the number of hauled out iguanas decreases with increasing solar elevation and THW index and increases with increasing tide height and hour of day, and accounts for over half of the variability in haulout at the site.

Models for Management

Models (13)–(20) show the relationship between haulout and environmental variables, but the prediction of future haulout requires advance knowledge of temperature and relative humidity. Models of particular relevance for management include only those environmental variables in $E(t)$ which are obtainable as long-range predictions. Table 4 reports these models; the best for each site are given here.

For the Sandy site, the model

$$N(t) = \frac{\beta(247.7 + 125.2\sin(0.4481(\text{day of year} + t/24)))}{1 + \alpha\left(\frac{S_e^{\varsigma}}{T^{\rho}}\right)}, \quad (21)$$

where β = 0.90210, α = 4.6447E-07, ς = 25.683, and ρ = 2.3556, yields an R^2 of 0.7244. Solar elevation alone accounts for 71% of the variability in haulout at the Sandy site (Table 4).

For the Rocky site, the model

$$N(t) = \frac{\beta S_e^{\xi}}{1 + \alpha\left(\frac{S_e^{\varsigma}}{H_r^{\xi} T^{\rho}}\right)}, \quad (19)$$

where β = 197.07, ι = 0.96393, α = 1.4863E-05, ζ = 21.849, ξ = 3.5498, and ρ = 3.0910, yields an R^2 of 0.5056. Solar elevation alone accounts for 38% of the variability in haulout at the Rocky site (Table 4).

Poisson Regression

Regression coefficients for each significant variable appear in Table 5. The overdispersion parameter estimates reported are either within or close to the range of values (1–4) that indicate a small amount of extra variation due to demographic stochasticity and lack of independence rather than inadequate model structure (Burnham and Anderson, 2002). However, using other measures in place of ambient temperature did not change the significance or direction of trends.

Sandy Site

All environmental variables present in the best Sandy site model (16) also were significant in the Poisson regression model for the Sandy site (Table 5).

Regression of Sandy site influx on the environmental variables yielded the following relationships: if all other variables are held constant, increases in solar elevation, positive shifts in wind direction (north to east, east to south, south to west, and west to north), wind speed, or dew point correspond to an increase in influx to the Sandy site; increases in tide height, seawater temperature, ambient temperature, percent relative humidity, or barometric pressure correspond to a decrease in influx to the Sandy site (Table 5).

Regression of Sandy site efflux on the environmental variables yielded the following relationships: increases in solar radiation, solar elevation, dew point, or barometric pressure correspond to an increase in efflux; increases in tide height, ambient temperature, percent relative humidity, or wind speed correspond to a decrease in efflux (Table 5).

Rocky Site

None of the environmental variables present in the Rocky site mathematical models with $\Delta_i < 10$ are significant in the regression model for the Rocky site (Table 5).

If all other variables are held constant, increases in solar radiation, seawater temperature, ambient temperature, or percent relative humidity correspond to a decrease in haulout at the Rocky site. Increasing dew point corresponds to an increase in haulout.

CHAPTER IV

DISCUSSION

Iguana Body Size

Foraging behavior and thermoregulation of small marine iguanas differ from those of larger individuals (White, 1973; Trillmich and Trillmich, 1986). Animals with estimated snout-to-vent lengths (SVL) ≤ 25 cm are considered "small" and are known to forage exclusively in the intertidal zones around low tide; animals with estimated SVL > 25 cm are designated as "large" and are more likely to forage in the subtidal zone (Buttemer and Dawson, 1993; Wikelski and Trillmich, 1994). For all observations in this study I differentiated between small and large iguanas by setting out 25 cm wooden size standards, each tied to a heavy rock. However, I later chose to combine numbers of small and large iguanas in the analysis for each site.

For Sandy site data, I made this choice for three reasons: (1) Small iguana flux only accounted for ~5% of the daily movement on average (unpublished data). (2) I could not objectively size some iguanas after several days because multiple size standards were either covered by sand or removed into the bay by wave action. (3) The few small animals that hauled out at the Sandy site typically failed to join the main group. Once out of the water they veered right or left toward the lava outcrops bordering the beach.

At the Rocky site, it was difficult to distinguish size due to the inherent foreshortening of each photograph. Several of the size standards also disappeared from this site and iguanas regularly hauled out over the standards that remained.

Effects of Diurnal Changes in Environmental Variables on Haulout

Although a *post hoc* test revealed that residuals for both sites are autocorrelated, the exceptionally high goodness-of-fit for the Sandy site model (16) and notably high goodness-of-fit for the Rocky site model (20) suggest the trends with environmental variables elucidated by these models are representative of the system. For both sites, all mathematical models with $\Delta_i < 10$ include solar elevation, tide height, and a measure of perceived temperature (Table 3). Poisson regression indicates the influence of several other environmental variables as well. Each environmental variable found to be significant at either site is discussed below.

Solar Radiation

Solar radiation does not appear in any of the best mathematical models (Table 3). The absence of solar radiation from the best mathematical models is consistent with other studies that show modal subtidal foraging times of large iguanas are unrelated to cloud cover or rock temperature (Buttemer and Dawson, 1993; Wikelski and Trillmich, 1994). Despite these findings, my regression analyses suggest that solar radiation does affect efflux and haulout (Table 5). In particular, as insolation increases, Sandy site efflux also increases and Rocky site haulout decreases.

Subjectively, solar radiation appeared to be the most important variable influencing efflux for the Sandy site. Few animals entered the water before the solar radiation reached 500 Wm^{-2}. On sunny mornings this often occurred by 08:30. On cloudy mornings, however, this level of solar radiation was not reached until 10:30 or later, resulting in a delay of efflux. If the increase in insolation was rapid (e.g., 350 Wm^{-2} to 950 Wm^{-2} within 10 min), iguanas moved to the water rapidly. During one such event, 97 iguanas entered the water in the first 10 min of a steep rise in insolation, and 96 entered during the next 10-min interval.

Using mirrors to artificially change insolation on individual marine iguanas elicits significant changes in thermoregulatory behaviors (White, 1973). If iguanas time their foraging so as to maximize rates of rewarming upon return to land, it would seem that solar radiation should be included in mathematical models describing haulout. Perhaps solar elevation, which was less variable than but highly correlated with solar radiation, functions as its proxy in the mathematical models.

Solar Elevation

Solar elevation is included in the best mathematical models for both sites (Table 3); indeed, models including only this environmental variable in the function $E(t)$ account for 71% and 38% of system variability for the Sandy and Rocky sites, respectively (Table 4).In all mathematical models for either site, as solar elevation increases to its maximal value, haulout decreases to its minimal value. Regression for the Sandy site suggests that as solar elevation increases, influx increases considerably (75% for a 10º increase in solar elevation), but efflux also increases at an even greater rate (89% for a 10º increase in solar elevation, Table 5). The decrease in the ratio of influx to efflux can be consistent with decreased haulout, depending on the particular values of influx and efflux. (For example, an influx of 4 iguanas and an efflux of 10 iguanas would, with an a 10º increase in solar elevation, change to an influx of 7 iguanas and an efflux of 19 iguanas, decreasing haulout an extra 6 iguanas. Whereas if the initial influx and efflux were 10 and 4, respectively, a 10º increase in solar elevation would increase haulout an extra 4 iguanas.)

Tide Height

All mathematical models suggest that haulout varies directly with tide height (Table 3). Marine iguanas are not efficient swimmers for vertebrates their size and have little stamina (Bartholomew et al., 1976; Dawson et al., 1977). Thus, fighting an outgoing tide upon return to a final haulout location is energetically expensive, especially with the dramatically lowered body temperatures experienced by iguanas returning from subtidal foraging bouts (Dawson et al., 1977; Trillmich and Trillmich, 1986). Consequently, riding the incoming tide may be cost effective for subtidal foragers, particularly on days with heavy surf. For intertidal foragers, increasing tide height decreases available foraging area; therefore high tides are expected to be correlated with increased haulout.

Regression results suggest that tide height is a significant predictor of Sandy site influx and efflux but not a significant predictor of Rocky site haulout (Table 5). In particular, as tide height increases, influx to and efflux from the Sandy site decrease. The rate of change in efflux is greater, resulting in an increase in the influx/efflux ratio (Table 5). This can be consistent with increased haulout, depending on the particular values of influx and efflux. The retarded influx as tide height increases may seem incongruous with the trend elucidated by the mathematical models, but it could be attributed to the variability larger iguanas contribute to the system. Although it may be most cost effective for subtidal foragers to ride the tide, their foraging opportunities are not restricted by low tide. Thus, even with increasing tide, subtidal foragers may leave the site to feed.

Seawater Temperature

No mathematical models for the Sandy site with $\Delta_i < 10$ include seawater temperature, but the fifth best mathematical model for the Rocky site includes this variable and depicts an indirect relationship (Table 3). Regression models for both sites include seawater temperature and depict an indirect relationship (Table 5): Sandy site influx and Rocky site haulout decrease as seawater temperature increases. Iguanas lose heat less rapidly in warmer water; increasing seawater temperature allows foraging sessions to be longer and rewarming periods to be less frequent than in cooler water. Because subtidal feeders have significantly longer foraging bouts than intertidal feeders, seawater temperature would be expected to have a stronger influence at locations where the majority of iguanas are subtidal feeders (Drent et al., 1999).

Although warmer seawater temperatures would enhance foraging over the short term, extended elevated seawater temperatures, as during El Niño events, are detrimental. Prolonged periods of warmer seawater magnify wave action, raise sea levels, and result in fewer available nutrients (Vinueza et al., 2006). This combination of factors is especially detrimental for intertidal herbivores which rarely forage in intense wave action (Trillmich and Trillmich, 1986; Wikelski and Trillmich, 1994). During El Niño years red and green algae, which constitute the majority of the marine iguana diet, diminish, and warmer-water, ephemeral species, typically brown algae, which are difficult for marine iguanas to digest, flourish (Laurie and Brown, 1990b; Wikelski and Thom, 2000). Marine iguanas rarely alter their feeding habits, making the absence of their preferred algal food source a problem of survival (Laurie, 1990; Wikelski and Trillmich, 1994; Romero and Wikelski, 2001). Marine iguanas actually can reduce their SVL under such conditions, a process that increases the odds of survival (Wikelski and Thom, 2000).

Average monthly seawater temperatures have been correlated with body condition index (body mass x SVL^{-3} x 10^6); if the body condition index drops below 35, high corticosterone levels result (Romero and Wikelski, 2001). Marine iguanas on Fernandina suffer higher mortality and have higher corticosterone levels than individuals on other islands in the archipelago during El Niño events. High levels of corticosterone over short periods can enhance survival, but if high levels are prolonged and body condition index drops below 25, death will result (Romero and Wikelski, 2001).

Ambient Temperature and Related Variables

All mathematical models for both study sites with $\Delta_i < 10$ contain either ambient temperature or other measures of perceived temperature such as wind chill, heat index, and THW index (Table 3). Moreover, as real or perceived temperature increases, fewer iguanas haul out. Regression results for both sites are congruous with this trend (Table 5).

Despite the presence of other measures of perceived temperature in the best mathematical models for each site, I used only ambient temperature as a regression factor. This was done because ambient temperature was collinear with the other measures of perceived temperature and it is not clear how other variables affect perception of heat by iguanas. For example, although heat index is present in the best Sandy site and second best Rocky site models, it may be a poor measure of perceived temperature for iguanas. Experiments have shown that iguanas lose little moisture cutaneously, potentially nullifying the effect water vapor content in air has on perceived temperature via evaporative cooling (Shoemaker and Nagy, 1984). Should high levels of insolation threaten to raise body temperature beyond the optimum 35ºC, extremely efficient postural changes keep body temperature within a range around the optimum. However, when prevented from assuming elevated basking postures, marine iguanas pant to offload heat after body temperature exceeds 40ºC (White, 1973). In this extreme case high water vapor content would negatively affect the efficacy of this uncommon cooling behavior.

Although it is unclear why some measures of perceived temperature perform better than ambient temperature in the mathematical models given the uncertain effects they have on perception of temperature by marine iguanas, it is clear that increasing temperatures, however they are perceived, correspond with decreased haulout.

Relative Humidity

All Sandy site mathematical models with $\Delta_i < 10$ depict a direct relationship between humidity and haulout (Table 3). Indeed, maximum haulout at the site occurred overnight when relative humidity was highest (Fig. 6, Fig. 3). Regression indicates that as relative humidity increases, with all other factors held constant, influx to the Sandy site decreases rapidly and efflux also decreases, although less rapidly (Table 5). The decrease in the ratio of influx to efflux is consistent with increased haulout when influx is small relative to efflux. By midafternoon, few iguanas left from or came to the Sandy site; the number of animals hauled-out largely stabilized (Fig. 6). Relative humidity, however, continued to increase throughout the afternoon and evening. This resulted in decreased influx and efflux later in the afternoon while relative humidity continued to increase, leading to maximum haulout at high values of relative humidity.

Haulout at the Rocky site did not reach its maximum overnight, as was observed at the Sandy site. Indeed, regression results suggest that increased relative humidity corresponds to decreased haulout at the Rocky site (Table 5). This could indicate that few marine iguanas use this site for final haulout—that is, iguanas stay overnight at the Rocky site only if conditions are unfavorable for return to their colony after their last foraging bout.

Equivalently, regression suggests that decreased relative humidity would correspond to increased haulout at the Rocky site. Lava rocks are known to reach temperatures of up to 60ºC (White, 1973). The resultant layer of warm dry air immediately above the rocks would have a high capacity to absorb water vapor, an optimum condition for rewarming a cold, wet iguana emerging from a foraging bout. A more rapid resumption of foraging is likely enabled by using sites with lava rock substrate for rewarming. The results from regression suggest that non-colony iguanas use the Rocky site for temporary haulout between foraging bouts.

Wind Direction and Wind Speed

No mathematical models with $\Delta_i < 10$ for either site include wind direction and one mathematical model with $\Delta_i < 10$ for the Sandy site includes wind speed (Table 3).

Regression suggests a positive shift in wind direction corresponds to increased influx at the Sandy site (Table 5). This site was more exposed to the dominant afternoon southwest to west–southwest winds (Fig. 3), whereas the Rocky site was more sheltered from these winds by a high basaltic outcrop. This difference may explain why haulout at the Sandy site was more sensitive to changes in wind direction.

For wind speed, the Sandy site mathematical model shows an indirect relationship between this variable and haulout (Table 3). Regression for the Sandy site shows the opposite trend: a direct relationship between wind speed and influx and an indirect relationship between wind speed and efflux (Table 5). The increase in influx/efflux ratio likely is always consistent with increased haulout.

Although I did not measure wave action, strong winds typically correlate with heavy surf. Even large iguanas have difficulty returning to shore in heavy surf, and wave action strongly influences foraging decisions by intertidal feeders (Dawson et al., 1977; Trillmich and Trillmich, 1986; Wikelski and Trillmich, 1994). Increased haulout would be expected since iguanas engaging in either foraging strategy likely would forage less when wave action is considerable. The Sandy site, although more exposed to dominant afternoon winds, is more sheltered from heavy surf than the Rocky site. In high winds, non-colony iguanas may preferentially haul out at the Sandy site because the beach makes for easier reentry onto land than do rocky crags.

Dew Point

None of the best mathematical models include dew point. Regression analyses for both sites, however, indicate the importance of this variable. At the Sandy site an increase in dew point is associated with an increase in influx and efflux. The rate of change in influx is greater, resulting in a slight increase in the influx/efflux ratio (Table 5). This can be consistent with increased haulout, depending on the particular values of influx and efflux. At the Rocky site, an increase in dew point is associated with an increase in haulout. When relative humidity in the afternoon is above 50%, as it always was at both sites, dew point makes a good predictor for minimum overnight temperature because reaching dew point halts the cooling process (Anonymous, 2009). A higher dew point throughout the day therefore indicates a warmer evening, providing iguanas with a longer time window in which to forage during the day. Increased numbers of iguanas foraging, or longer foraging time windows, allow more iguanas to be hauled out at alternate sites.

Thus, with increased dew point, the corresponding slight increase in haulout at both sites may be due to increased numbers of non-colony iguanas hauling out.

Barometric Pressure

None of the best mathematical models include barometric pressure, but regression analysis for the Sandy site suggests that increased barometric pressure is associated with decreased influx and increased efflux (Table 5). This suggests higher barometric pressure corresponds to decreased haulout. Consequently, lower barometric pressure corresponds to increased haulout at the Sandy site, as expected given that decreasing barometric pressure is associated with deteriorating weather conditions.

Maximal Haulout

Maximal daily haulout at the Sandy site was circumscribed by tide, with the highest haulouts occurring around neap tide (10 May 2011, day of year 130, Fig. 4) and the lowest around spring tide (16 May, day of year 136, Fig. 4). The large range in daily maximal haulout (160 to 300 iguanas) at the Sandy site (Fig. 4) may be due to intermittent use by non-colony subtidal foragers. Although in general marine iguanas exhibit sleeping and resting site fidelity (Wikelski, 1999; Romero and Wikelski, 2002), subtidal foragers may swim 400 m from their colony and stay overnight at non-colony locations if returning to their colony is environmentally unfavorable (Gleeson, 1979; Trillmich and Trillmich, 1986). During spring tides the dry area above the high tide line decreases, potentially limiting haulout by non-colony visitors. At the Sandy site, iguanas often hauled out in a “train” that extended from just above the water line to the salt bush; high tide during spring tides would limit the length of the train (Fig. 1). Furthermore, during low spring tide iguanas would have to travel nearly 30 m between the favored haulout site near the salt bush and the water line. Given that the metabolic cost of walking is approximately four times that of swimming at the same speed (Gleeson, 1979), this also might make the site unfavorable for haulout by non-colony marine iguanas.

Because the Rocky site was a sample area of a larger haulout region and animals could enter and leave its boundaries from directions other than the sea, there was little or no circumscribing effect of tide on maximal daily haulout (Fig. 4B). Furthermore, Rocky site haulout was not maximized at the beginning and end of each day as was Sandy site haulout. Haulout numbers increased from the first haulout count of the day before falling to the daily minimum, and then increased above the final haulout count value before decreasing to that value at nightfall (Fig. 8). This occurred because the site was a thoroughfare to the sea. As solar elevation increased in the morning, the number of iguanas passing through the site increased until all iguanas left to forage. As solar elevation decreased in the evening, iguanas hauling out at locations beyond the site passed through, temporarily increasing observed haulout numbers. This motivated the choice of solar elevation as the functional form (1b) circumscribing maximal haulout at this site.

Caveats

Inferring Occupancy

Inferred occupancies for some evenings and ensuing mornings were markedly mismatched at the Sandy site (Fig. 6). This was unexpected because iguanas are known to be fairly inactive overnight (Nagy and Shoemaker, 1984; Buttemer and Dawson, 1993) and iguanas did not appear to leave the Study site by alternate routes. It is possible that the iguanas left from or arrived at the bushes via non-monitored routes, but given the significantly higher energetic cost of walking versus swimming this seems unlikely (Gleeson, 1979). Additionally, non-breeding marine iguanas are found exclusively on the shoreline (Darwin, 1839; Carpenter, 1966), and the only haulout sites that would not have required overland travel were to the east. Because haulout at the site was always concentrated at the western end (Fig. 1), iguanas would have to walk through the monitored site to reach other haulout sites. Only 10 iguanas did this over the study period (pers. obs.).

For some days when inferred occupancies were artificially low, adding the absolute value of the most negative inferred occupancy to all other occupancies for that day compounded overnight mismatches. In other cases the addition ameliorated preexisting mismatches. Two factors may exacerbate any real mismatch. First, the fact that the majority of iguanas at the site were large, and therefore do not necessarily feed every day, may contribute to this phenomenon (Trillmich and Trillmich, 1986). If on a particular day x iguanas hauled out, entered the salt bush, and did not leave the site to forage the following day, an overnight mismatch of x iguanas would result because inferring occupancies back from the next day's census would not account for those iguanas. Second, tallying iguanas entering the water (leaving the site) required higher vigilance than tallying those exiting (hauling out). Thus, any observer error would tend to inflate inferred occupancies following the census and depress those before it.

The phenomenon of mismatched overnight occupancies arose not only at the Sandy site, however, but also at the Rocky site, where haulout was photographed and not inferred (Fig. 8). This suggests the mismatch was inherent to the system and was not merely the result of observer error. Iguanas may have left the site overnight. A longer study period is needed for teasing out patterns in the overnight disparities, as well as identifying and isolating the contributing factors.

Validity of Assumption Five

Assumption five presupposes that recovery after disturbance is rapid, but this assumption has no empirical support at this point. Indeed, no disturbances occurred during my study. The arrival of sea lions, sea turtles, fur seals, cormorants, and other fauna did not lead to changes in compartment occupancy. The shallow depth of Sea Lion Bay and an underwater basaltic ridge at its mouth precludes the entrance of sharks, which are known predators of marine iguanas (Dawson et al., 1977). The presence of a shark might lead to a disturbance, but even at the unprotected Rocky site such a disturbance was never observed. Humans and feral animals such as dogs, which elicit a rapid fleeing response from iguanas (Kruuk and Snell, 1981), have no standing populations on Fernandina and researchers never approached the iguanas at either site during the study period.

Implications for Management

Mathematical models can help managers choose the best times for tourists to visit a site with the least impact on iguanas or choose times to make population estimates. The accuracy of long-range model predictions depends on whether the environmental variables included in the function $E(t)$ can be reliably obtained well in advance (Henson et al., 2006). Variables such as solar elevation, hour of day, and tide height meet this criterion. Other variables, such as temperature and wind speed, when obtained in advance, are at best accurate only for the near future and are reliable only as historical measurements. None of the models with $\Delta_i < 10$ were dependent only on environmental variables that can be reliably obtained well in advance. However, such models still account for a large amount of system variability (Table 4).

In previous studies, counts to achieve population estimates were taken just after low tide because these times were assumed to coincide with maximum haulout (Romero and Wikelski, 2001). Although this may be true for populations comprised largely of intertidal feeders, at sites with mostly subtidal feeders, mathematical models indicate that counts made on a warm, late afternoon near high tide would provide the most reliable population estimate. Moreover, the mathematical models used here lend themselves to straightforward estimation of the total number of marine iguanas that use a site for haulout. If I_o iguanas are observed hauled out at a site at time t, then from equations (5)–(6) the total number of iguanas that may choose to haul out at the site is $I_o(1+\alpha E(t))$. When $E(t)$ depends only on environmental variables that can be reliably obtained well in advance, a table of "correction factors" of the form $1+\alpha E(t)$ for different times of day and year can be generated to allow for rapid colony size estimates from observed haulout. In this way, trends in marine iguana population size could be quantified by monitoring changes at key haulout sites.

This study suggests the following recommendations for managers.

1. The functional forms of modeling envelopes (assumption 4) should be tested for a longer time period, ideally at different times of year.

2. A unit that records running averages of solar radiation would provide a smoother and therefore more useful measure of this variable for modeling purposes.
3. Assuming the presence of sufficient numbers of small animals, models incorporating iguana size should be developed for haulout sites.
4. A measure of wave action (e.g. Wikelski and Trillmich, 1994) should be included as a variable in future models. Although sea motion has little effect on subtidal feeders, it inhibits foraging by intertidal feeders (Trillmich and Trillmich, 1986).
5. The methodology should be applied at a site impacted by humans. Measured corticosterone levels are lower in marine iguanas at sites impacted by humans (Romero and Wikelski, 2002). If human presence correlates with changes in marine iguana physiology, behavioral changes also may occur.

Strength of Modeling Methodology

Compartmental differential equation models have been used for over a decade to provide nuanced understanding of observed dynamic patterns in marine birds and mammals (Henson and Hayward, 2010). This study affirms the portability of the methodology to a taxon distantly related to those studied previously. Differential equation models for both the Sandy and the Rocky sites are capable of predicting haulout dynamics with a high level of accuracy and demonstrate that much of the variability in haulout can be understood by the concurrent, diurnal fluctuations in the abiotic environment. That is, knowing the values of certain environmental variables at a given time t allows accurate prediction of haulout at time t.

The Rocky site models are not as accurate as the Sandy site models. Maximum and minimum daily haulout at the Rocky site were highly variable (Fig. 8). However, mathematical models and regression analysis still elucidate relationships between this variability and environmental variables. Use of the Rocky site as a thoroughfare increased variability at this site, although changes in solar elevation capture much of the trend in daily maximal haulout. Probable use of the Rocky site by non-colony iguanas for warming, the dynamics of which appear to vary with relative humidity, measures of perceived temperature, and dew point, also likely increased variability in minimum daily haulout. Length of these warming periods may vary with cloud cover or insolation, further increasing daily variability (Wikelski and Trillmich, 1994).

Both the time of year and seawater temperature data suggest the current study was conducted during the transition time between seasons, and thus may not reflect what happens at other times of the year. Although the temporal applicability is not certain, the Sandy site model, when applied to the independent validation data set without reparameterizing, still achieved a very high goodness-of-fit. That is, parameter values estimated from the estimation data set accounted for 80% variability in the (independent) validation data set. This indicates that the essential dynamics of haulout are predictable as functions of environmental variables.

CHAPTER V

CONCLUSION

Temporal dynamics of Galapagos marine iguana haulout are highly deterministic. Numbers of hauled-out animals can be predicted with a high level of accuracy given environmental data. Multiple environmental variables influence haulout dynamics, with solar elevation and tide height accounting for a large portion of the variability. Measures of temperature improve model accuracy and allow a more nuanced understanding of haulout, but they are less amenable to making long-range predictions beneficial for management. Mathematical models not only contribute to an understanding of the ecology and temporal dynamics of marine iguana haulout and foraging, but also can be used to quantify population trends in marine iguanas. For a threatened endemic species, the ability to monitor these trends is important. Given the success of using compartmental differential equations to explain, describe, and predict dynamics of animal behavior across multiple taxa, it is reasonable to assume the technique could help in the development of conservation measures for this and other threatened species.

Table 1. Environmental Variables.

Environmental factor	Variable
Solar radiation	$S_r\ (t)$
Solar elevation	$S_e\ (t)$
Tide Height	$T\ (t)$
Seawater temperature	$S_p\ (t)$
Ambient temperature	$A\ (t)$
Relative humidity	$H_u\ (t)$
Dew point	$D\ (t)$
Wind speed	$W_s\ (t)$
Wind direction	$W_d\ (t)$
Wind chill	$W_c\ (t)$
Heat index	$H_x\ (t)$
THW index	$T_x\ (t)$
Barometric pressure	$B\ (t)$
Hour of day	$\mathrm{H_r}\ (t)$

Note: Each environmental variable X was nondimensionalized and scaled so that $1 \leq X \leq 2$.

Table 2. Descriptive Statistics for Environmental Variables Over Study Period.

Variable	Minimum	Maximum	Average	Unit
$S_r\ (t)$	1	1230	537.4	W/m2
$S_e\ (t)$	-0.9	68.1	46.14	º above horizon
$T\ (t)$	0.3	1.83	1.12	meters
$S_p\ (t)$	20.5	24.7	22.1	ºC
$A\ (t)$	22.7	31.3	28.1	ºC
$H_u\ (t)$	55	99	76.8	% relative
$D\ (t)$	20	25.8	23.5	ºC
$W_s\ (t)$	0	25.7	14.1	m/s
$W_d\ (t)$	15	360	190.1	º on circular scale
$W_c\ (t)$	22.7	31.2	27.6	ºC
$H_x\ (t)$	24.2	36.6	32.0	ºC
$T_x\ (t)$	24.2	36.2	31.5	ºC
$B\ (t)$	753.7	759.9	756.9	mm/hg

Table 3. Best Environmental Functions: Sandy and Rocky Sites. The environmental variables are as described in Table 1. Increasing variables in the denominator of *E*(*t*) yields increased haulout and increasing variables in the numerator of *E*(*t*) yields decreased haulout. Asterisks denote the best model in for each site.

Sandy site				Rocky site			
$E(t)$	σ^2	Δ_i	R^2	$E(t)$	σ^2	Δ_i	R^2
$\frac{S_e^{\varsigma} H_x^{\phi}}{H_u^{\psi} T^{\rho}}$	5.89	0.000	0.7713*	$\frac{S_e^{\varsigma} T_x^{\omega}}{H_r^{\xi} T^{\rho}}$	5.41	0.000	0.5671*
$\frac{S_e^{\varsigma} T_x^{\omega}}{H_u^{\psi} T^{\rho}}$	5.90	0.3478	0.7711	$\frac{S_e^{\varsigma} H_x^{\phi}}{H_r^{\xi} T^{\rho}}$	5.42	0.4943	0.5665
$\frac{S_e^{\varsigma} A^{\zeta}}{H_u^{\psi} T^{\rho}}$	5.90	0.7241	0.7709	$\frac{S_e^{\varsigma} W_c^{\varphi}}{H_r^{\xi} T^{\rho}}$	5.56	9.550	0.5556
$\frac{S_e^{\varsigma} W_c^{\varphi}}{H_u^{\psi} T^{\rho}}$	5.92	1.468	0.7705	$\frac{S_e^{\varsigma} A^{\zeta}}{H_r^{\xi} T^{\rho}}$	5.64	14.46	0.5495
$\frac{S_e^{\varsigma}}{H_u^{\psi} T^{\rho}}$	5.95	1.670	0.7691	$\frac{S_e^{\varsigma} S_p^{\mu}}{H_r^{\xi} T^{\rho}}$	5.71	18.95	0.5438
$\frac{S_e^{\varsigma} W_s^{\lambda}}{H_u^{\psi} T^{\rho}}$	5.95	3.667	0.7691				

Table 4. Models for Management: Sandy and Rocky Sites. The environmental variables are as described in Table 1. Increasing variables in the denominator of *E*(*t*) yields increased haulout and increasing variables in the numerator of *E*(*t*) yields decreased haulout. Δ_i values are in reference to best models for each site as given in Table 3.

Sandy site				Rocky site			
$E(t)$	σ^2	Δ_i	R^2	$E(t)$	σ^2	Δ_i	R^2
$\frac{S_e^{\varsigma}}{T^{\rho}}$	7.10	68.0	0.7244	$\frac{S_e^{\varsigma}}{H_r^{\xi} T^{\rho}}$	6.18	46.1	0.5056
S_e^{ς}	7.55	89.9	0.7068	$\frac{S_e^{\varsigma}}{T^{\rho}}$	6.34	53.2	0.4929
				$\frac{S_e^{\varsigma}}{H_r^{\xi}}$	7.51	114.3	0.3998
				S_e^{ς}	7.76	124.3	0.3796

Table 5. Poisson Regression Analysis: Sandy and Rocky Sites. Coefficients are shown only for significant factors ($p < 0.05$). Increasing an environmental variable by C, all else held equal, causes a corresponding P percent change in the output. Positive coefficients indicate a direct relationship and negative coefficients indicate an indirect relationship.

		Sandy site					**Rocky site**	
		Influx		Efflux		Influx/Efflux	Haulout	
Variables	C (↑)	β	P	β	P	P	β	P
$S_r(t)$	200 w/m^2	-		0.001*	27 (↑)	-	-0.0005*	10 (↓)
$S_e(t)$	10.0º	0.056*	75 (↑)	0.064*	89 (↑)	7 (↓)	-	
$T(t)$	0.5 m	-0.320	15 (↓)	-1.010*	40 (↓)	40 (↑)	-	
$S_p(t)$	0.5º C	-0.633*	27 (↓)	-		-	-0.093*	5 (↓)
$A(t)$	1.0º C	-1.437	76 (↓)	-1.408	76 (↓)	3 (↓)	-0.465*	37 (↓)
$H_u(t)$	5.0 %	-0.377*	85 (↓)	-0.323	80 (↓)	24 (↓)	-0.108*	42 (↓)
$W_d(t)$	22.5º	0.006	15 (↑)	-		-	-	
$W_s(t)$	5.0 m/s	0.046*	26 (↑)	-0.0588*	25 (↓)	69 (↑)	-	
$D(t)$	0.1º C	1.805*	20 (↑)	1.337	14 (↑)	5 (↑)	0.436*	4 (↑)
$B(t)$	1.0 mm Hg	-0.740*	52 (↓)	0.244*	28 (↑)	62 (↓)	-	
Coefficient of Dispersion		3.016		4.218		-	5.618	

* $p < 0.01$

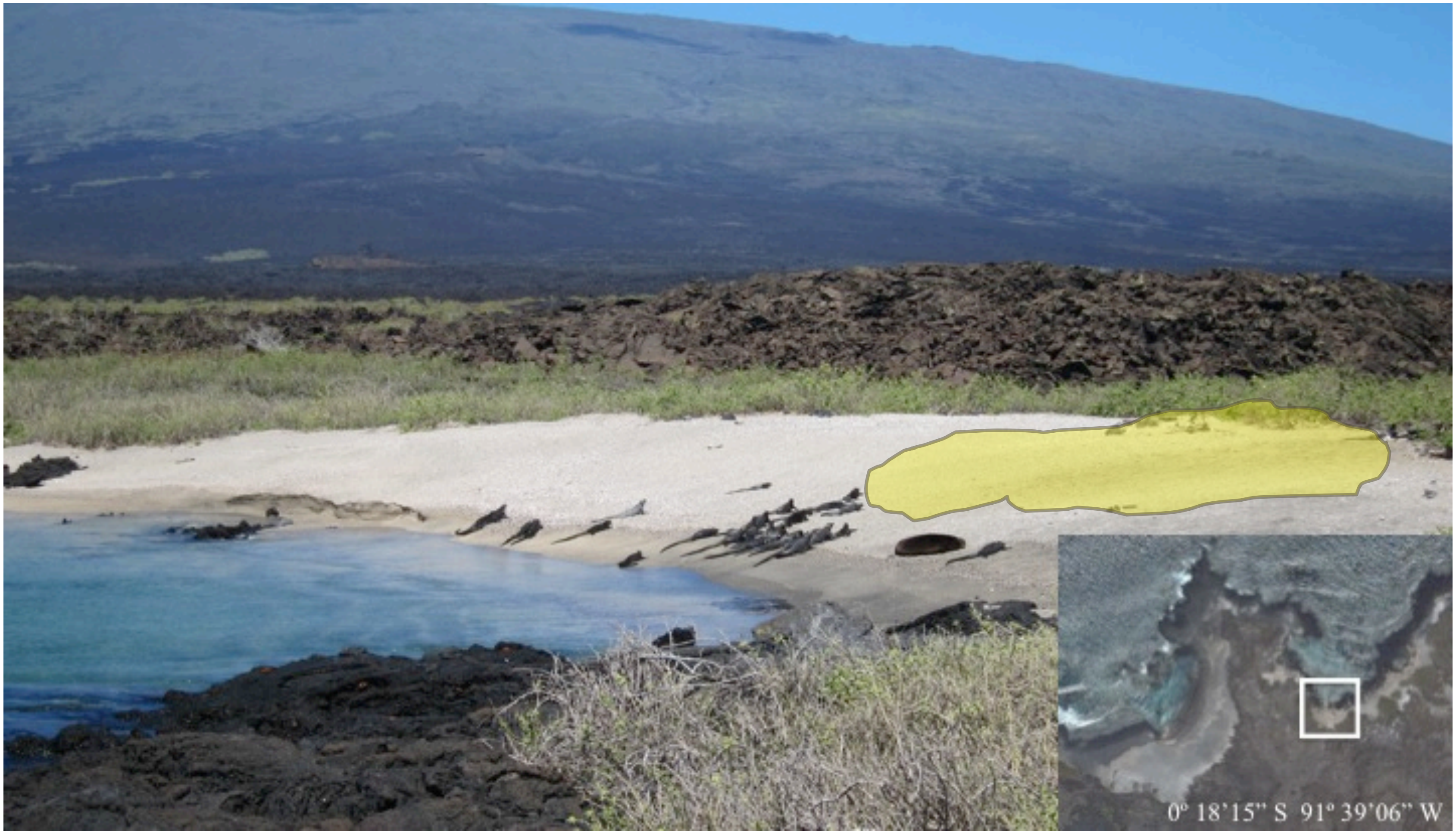

Fig. 1. Sandy site.

Sandy study site just off Sea Lion Bay of Cabo Douglas (inset) on Isla Fernandina of the Galápagos Archipelago. The beach pictured was a final haulout site for hundreds of iguanas, with iguanas concentrated in the region indicated in yellow and the surrounding salt bush (*Cryptocarpus pyriformis*) toward evening. Concentrated haulout each day extended to just above the high water line that day.

Fig. 2. Rocky site.

Rocky study site on the tip of Cabo Douglas (inset) on Isla Fernandina of the Galápagos Archipelago. Only iguanas within the area demarcated by the white perimeter are included in counts derived from photographs. Iguanas with > $^{2}/_{3}$ of their bodies, tails not included, within the area were counted (Table A-2). This picture shows the site at high tide.

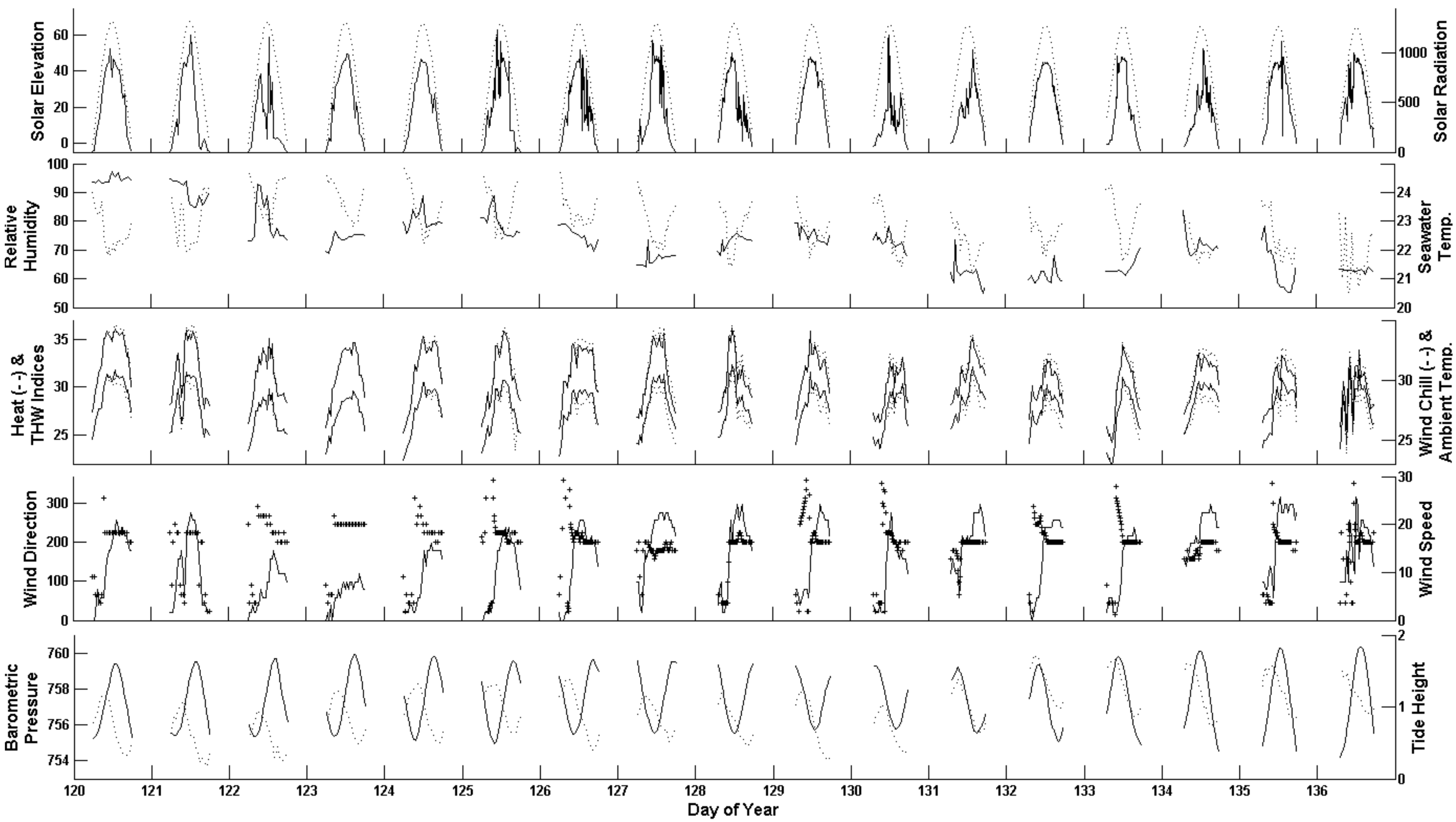

Fig. 3. Trends in environmental variables.

Each variable is graphed against time, represented by day of year. Except for wind chill, all variables on the right (solar radiation, seawater temperature, ambient temperature, wind speed, and tide height) and THW index are represented by black lines. Heat and THW index values covary tightly and are above wind chill and ambient temperature in the third graph, which also covary tightly.

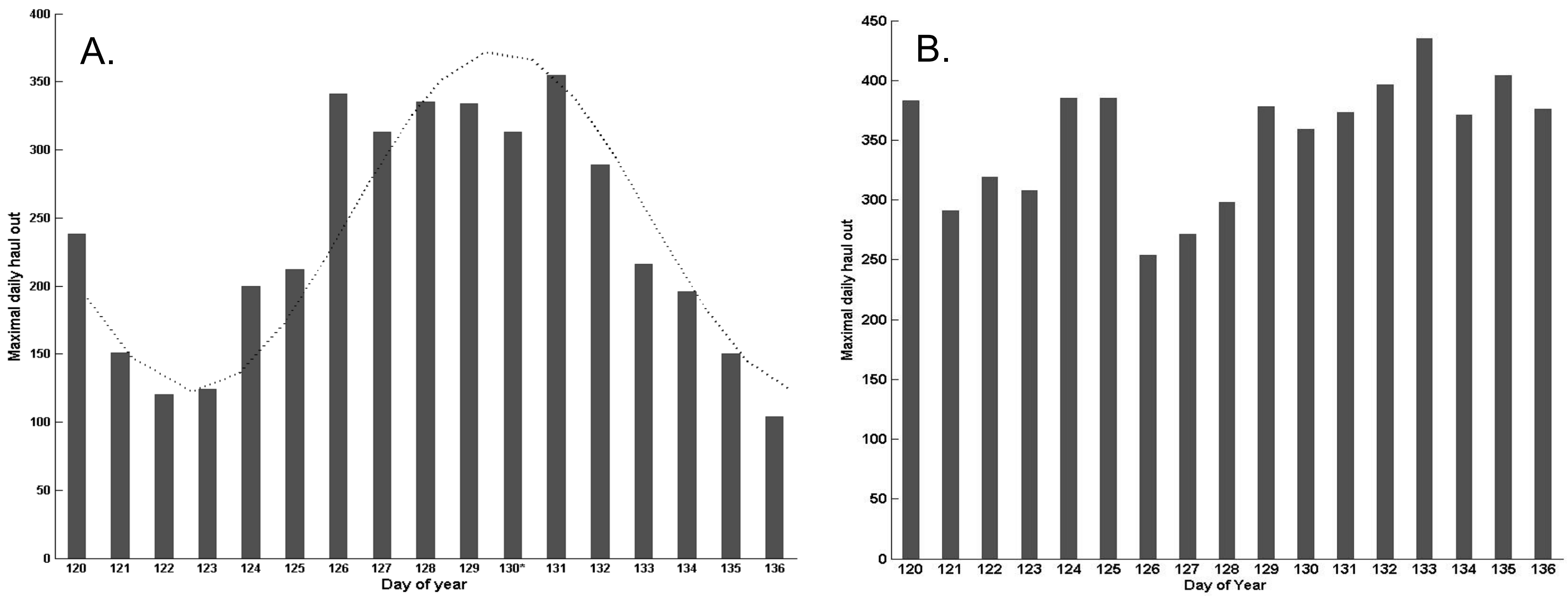

Fig. 4. Maximal daily haulout.

A. Maximal daily haulout counts at the Sandy site over the 17 day study period starting on the 30 April, 2011. The dotted line represents equation (1a). B. Maximal daily haulout for the Rocky site.

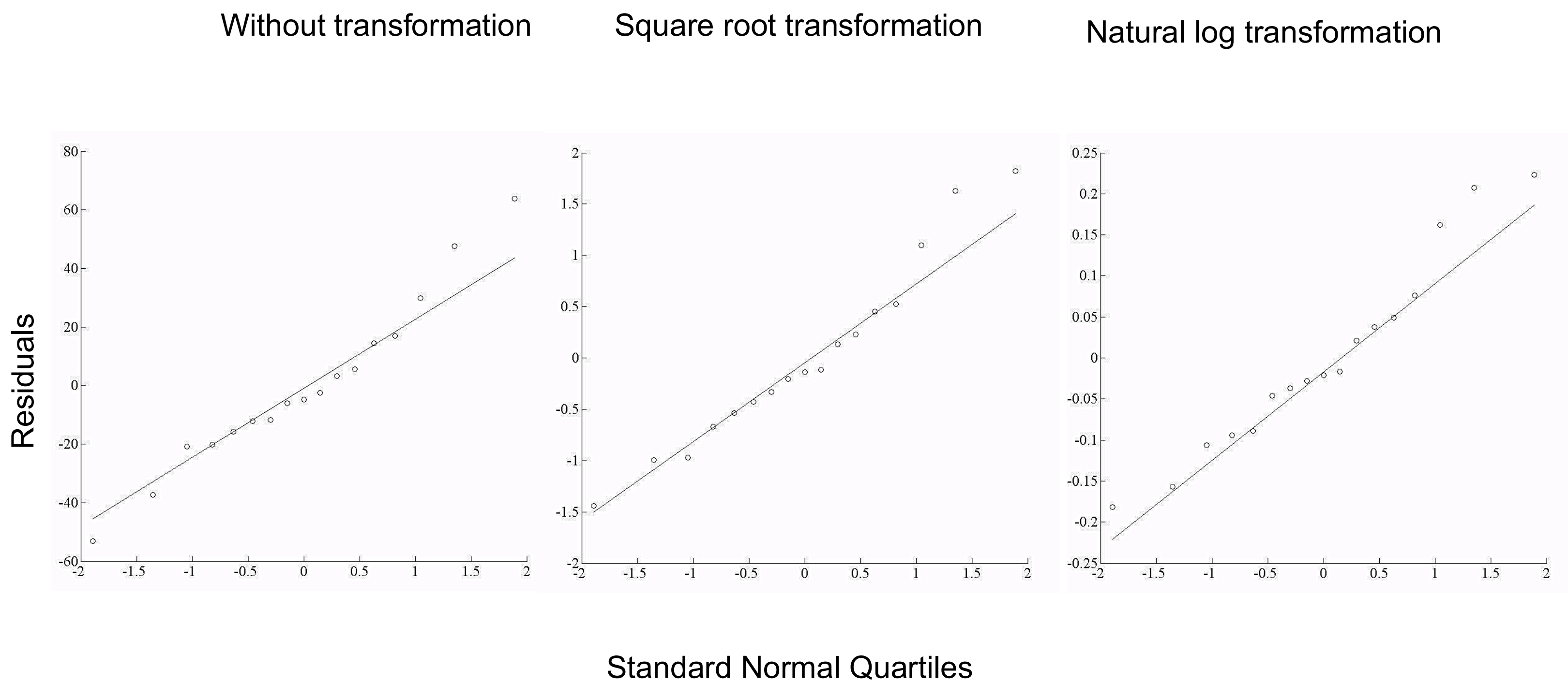

Fig. 5. QQ plots for equation (1a): Sandy site.

QQ plots of untransformed residuals, square root transformed residuals, and log transformed residuals were used to graphically evaluate residuals for normal distribution. Here, the residuals of submodel (1a), the functional form proportional to the number of iguanas eligible to haulout at the Sandy site, are evaluated. Normality would be confirmed by a linear relationship between the residual and the normal distribution. Circles represent each residual. The solid line joins the first and second quartiles, demarking the predicted slope if the distribution is normal.

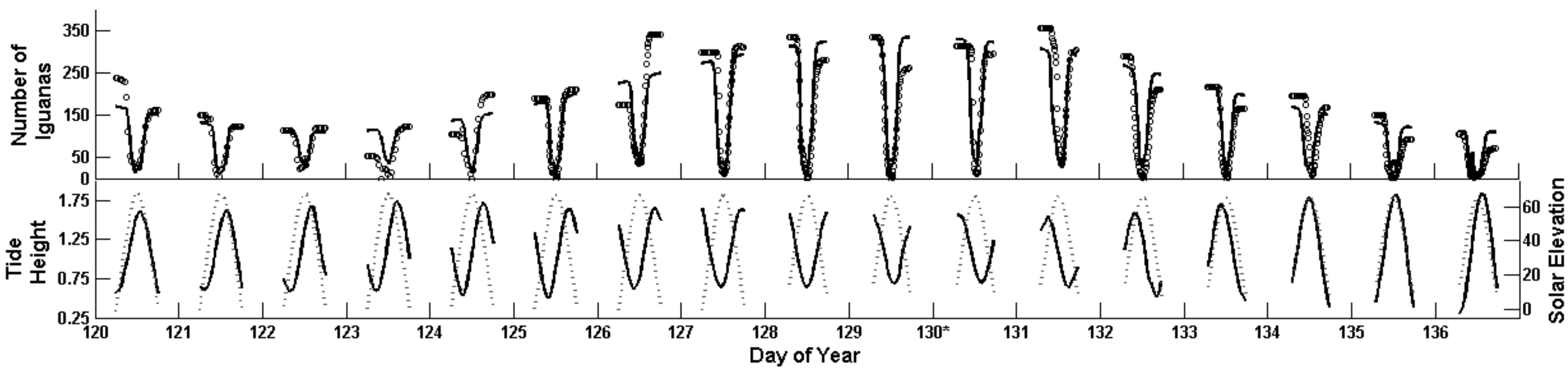

Fig. 6. Best model: Sandy site.

Model predictions (solid line) are graphed with census and inferred occupancy data (circles). Solar elevation (dashed line) and tide height (solid line), the most descriptive variables for the system, are graphed below model and occupancy data for reference. An asterisk denotes neap tide.

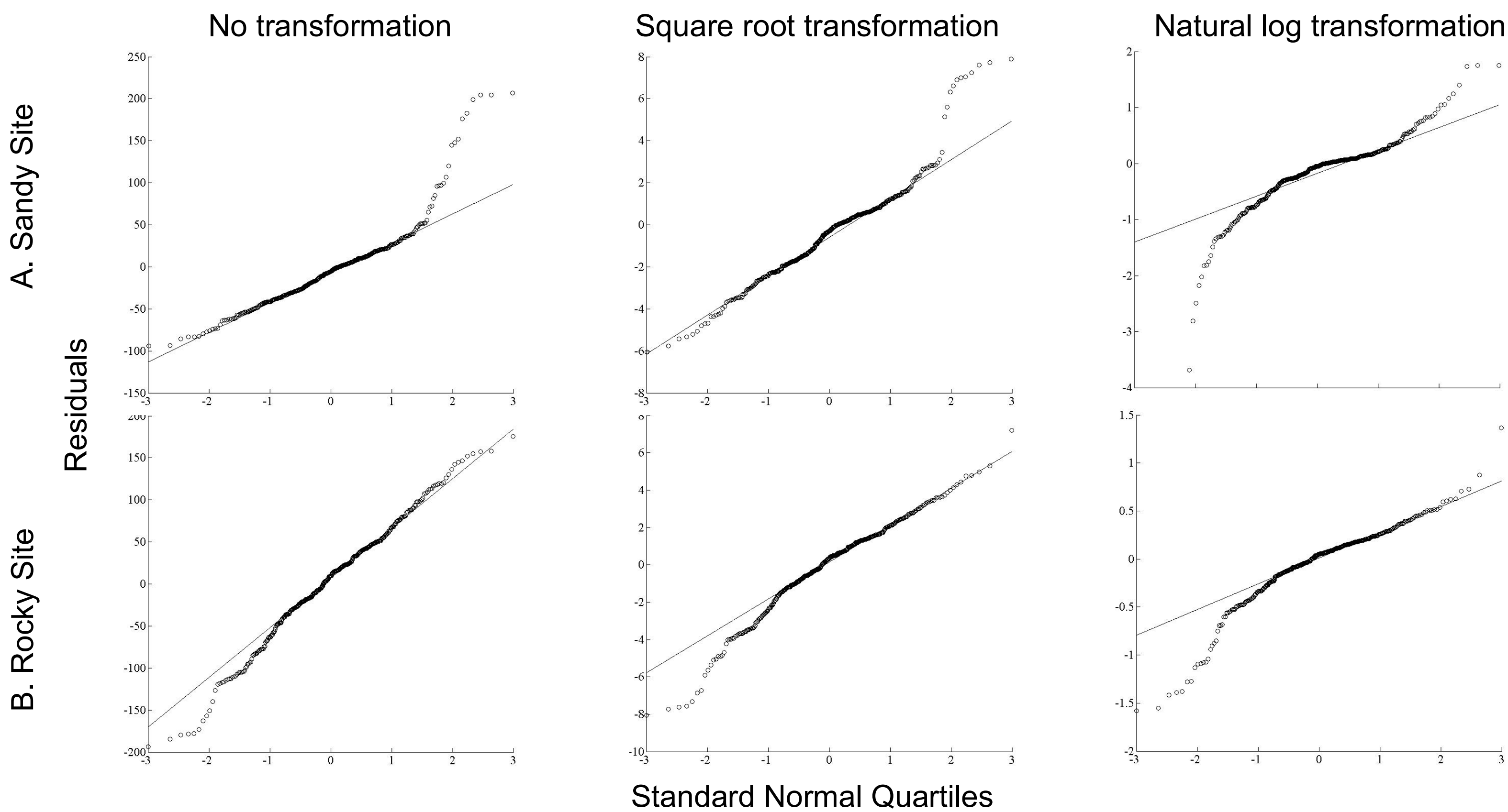

Fig. 7. QQ plots: Best models for Sandy and Rocky sites.

QQ plots of untransformed residuals, square root transformed residuals, and log transformed residuals of the best models for each site were used to graphically evaluate residuals for normal distribution. Normality would be confirmed by a linear relationship between the residual and the normal distribution. Circles represent each residual. The solid line joins the first and third quartiles.

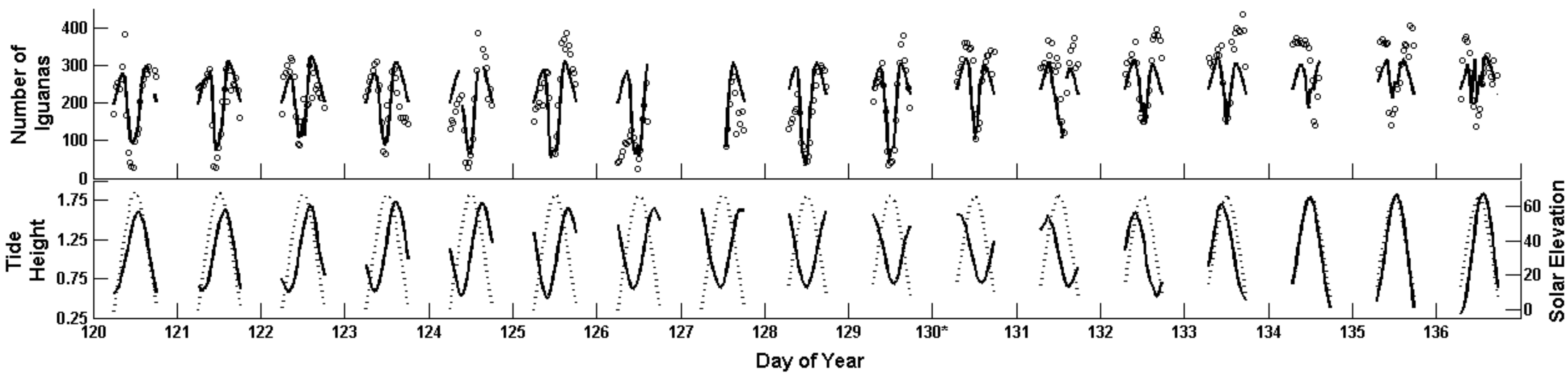

Fig. 8. Best model: Rocky site.

Model predictions (solid line) are graphed with census and inferred occupancy data (circles). Solar elevation (dashed line) and tide height (solid line), the most descriptive variables for the system, are graphed below model and occupancy data for reference. An asterisk denotes neap tide. Breaks in the model prediction occur where photographs were lost or data were excluded from analysis (see Methodology).

APPENDIX A

ADDITIONAL DATA

Table A- 1. Negative Inferred Occupancies. Time intervals for which extrapolating inferred occupancies generated negative numbers of iguanas. Corrected values are the inferred occupancy plus the most negative inferred occupancy of the day (in gray). Though not all shown here, each occupancy for affected days also was corrected. Corrected values replaced inferred occupancy in the data set for the given day of year and time interval. Days are separated by dashed lines.

Day of year	Time	Inf. occ.	Corr. value
123	1000	-11	0
123	1230	-5	6
124	1030	-3	45
124	1100	-17	31
124	1130	-36	12
124	1200	-48	0
124	1230	-28	20
125	1200	-2	8
125	1210	-6	4
125	1220	-10	0
125	1230	-6	4
128	1120	-2	33
128	1130	-8	27
128	1140	-13	22
128	1150	-22	13
128	1200	-30	5
128	1210	-34	1
128	1220	-35	0
128	1230	-31	4
128	1240	-25	10
128	1250	-18	17
128	1300	-3	32
129	1110	-12	45
129	1120	-25	32
129	1130	-36	21

Day of year	Time	Inf. occ.	Corr. value
129	1140	-47	10
129	1150	-49	8
129	1200	-50	7
129	1210	-50	7
129	1220	-57	0
129	1230	-55	2
129	1240	-48	9
129	1250	-40	17
129	1300	-29	28
129	1310	-13	44
132	1130	-5	16
132	1140	-7	14
132	1150	-8	13
132	1200	-13	8
132	1210	-15	6
132	1220	-20	1
132	1230	-19	2
132	1240	-21	0
132	1250	-13	8
132	1300	-5	16
132	1310	-3	18
133	1200	-4	9
133	1210	-2	11
133	1220	0	13
133	1230	-13	0

Day of year	Time	Inf. occ.	Corr. value
133	1240	-12	1
133	1250	-3	10
135	1030	-13	34
135	1040	-22	25
135	1050	-26	21
135	1100	-27	20
135	1110	-30	17
135	1120	-34	13
135	1130	-39	8
135	1140	-42	5
135	1150	-43	4
135	1200	-45	2
135	1210	-47	0
135	1220	-46	1
135	1230	-47	0
135	1240	-44	3
135	1250	-37	10
135	1300	-38	9
135	1310	-34	13
135	1320	-31	16
135	1330	-25	22
135	1340	-20	27
135	1350	-17	30
135	1400	-13	34
135	1410	-2	45

Table A- 2. Entire Data Sets for Haulout: Sandy and Rocky Sites. Inferred occupancies are given for the Sandy site; an * marks data used in the validation data set. Counts generated from photographs are given for the Rocky site. Day of year 120 is equivalent to April 30.

Day of Year	Time	Sandy	Rocky	Day of Year	Time	Sandy	Rocky
120	600	238	172	121	1300	38	205
120	630	237	242	121	1330	53	236
120	700	236	253	121	1400	73	291
120	730	234	238	121	1430	95	202
120	800	232 *	263	121	1500	117 *	285
120	830	229	296	121	1530	124 *	234
120	900	191	383	121	1600	123	251
120	930	111 *	166	121	1630	123	245
120	1000	52	67	121	1700	123	265
120	1030	41 *	42	121	1730	124 *	232
120	1100	35 *	32	121	1800	124 *	162
120	1130	30 *	27	122	600	115	169
120	1200	27	99	122	630	115 *	269
120	1230	31 *	116	122	700	115 *	279
120	1300	45	132	122	730	114	298
120	1330	64 *	205	122	800	113 *	284
120	1400	87	246	122	830	110 *	319
120	1430	123 *	262	122	900	104	313
120	1500	142	288	122	930	82	269
120	1530	151 *	276	122	1000	45	165
120	1600	158 *	295	122	1030	23	90
120	1630	160 *		122	1100	26	87
120	1700	161		122	1130	27 *	151
120	1730	163	287	122	1200	47	211
120	1800	163 *	270	122	1230	33	155
121	600	151 *	241	122	1300	48 *	193
121	630	150	242	122	1330	64 *	198
121	700	150 *	247	122	1400	76	300
121	730	149	248	122	1430	95	212
121	800	144 *	255	122	1500	118	278
121	830	142	276	122	1530	120 *	236
121	900	141 *	271	122	1600	120 *	247
121	930	107	290	122	1630	120	228
121	1000	37 *	140	122	1700	120 *	214
121	1030	20	32	122	1730	120	215
121	1100	10 *	29	122	1800	120 *	186
121	1130	6 *	53	123	600	52	217
121	1200	19 *	82	123	630	52 *	234
121	1230	23	118	123	700	52 *	258

Day of Year	Time	Sandy	Rocky	Day of Year	Time	Sandy	Rocky
123	730	52 *	271	124	1700	200 *	211
123	800	52 *	287	124	1700	200 *	211
123	830	51 *	303	124	1730	200 *	237
123	900	46	308	124	1800	200	192
123	930	32 *	232	125	600	190 *	151
123	1000	0	245	125	630	190 *	182
123	1030	23 *	146	125	700	190	189
123	1100	22 *	71	125	730	190 *	199
123	1130	19 *	64	125	800	190 *	241
123	1200	12	193	125	830	190 *	193
123	1230	6 *	157	125	840	190 *	
123	1300	14 *	241	125	850	190	
123	1330	47	284	125	900	190 *	254
123	1400	67 *	289	125	910	190 *	
123	1430	96	265	125	920	189	
123	1500	112	227	125	930	186 *	282
123	1530	118	191	125	940	184 *	
123	1600	118	162	125	950	167	
123	1630	122	161	125	1000	126 *	281
123	1700	122	149	125	1010	86 *	
123	1730	122 *	159	125	1020	66 *	
123	1800	124	143	125	1030	53	212
124	600	104	131	125	1040	40 *	
124	630	104 *	155	125	1050	25 *	
124	700	104	148	125	1100	19	73
124	730	104 *	176	125	1110	15 *	
124	800	104 *	196	125	1120	13	
124	830	103 *	210	125	1130	14	68
124	900	95		125	1140	14	
124	930	118	219	125	1150	12	
124	1000	60	129	125	1200	8	63
124	1030	45	42	125	1210	4 *	
124	1100	31 *	29	125	1220	0 *	
124	1130	12 *	41	125	1230	4	112
124	1200	0	62	125	1240	11	
124	1230	20 *	105	125	1250	24	
124	1300	65	209	125	1300	47 *	194
124	1330	113	287	125	1310	70 *	
124	1400	142	385	125	1320	80 *	
124	1430	174 *		125	1330	101 *	264
124	1500	186		125	1340	117	
124	1530	191 *	344	125	1350	133	
124	1600	194	322	125	1400	161 *	360
124	1630	197	292	125	1410	168 *	

Day of Year	Time	Sandy	Rocky
125	1420	183 *	
125	1430	185 *	368
125	1440	192	
125	1450	198	
125	1500	200 *	341
125	1530	208	385
125	1600	212	351
125	1630	210	329
125	1700	210 *	288
125	1730	210	281
125	1800	210	250
126	600	175 *	42
126	630	175	45
126	700	175	59
126	730	175 *	71
126	800	175 *	93
126	830	175	92
126	840	175	
126	850	175	
126	900	175	97
126	910	174 *	
126	920	173	
126	930	162 *	113
126	940	145	
126	950	130	
126	1000	113 *	126
126	1010	97 *	
126	1020	82 *	
126	1030	75	108
126	1040	71 *	
126	1050	64 *	
126	1100	61 *	87
126	1110	60 *	
126	1120	54 *	
126	1130	52	25
126	1140	39 *	
126	1150	35	
126	1200	39 *	52
126	1210	39	
126	1220	38 *	
126	1230	38 *	76
126	1240	45	
126	1250	52	
126	1300	80	157
126	1310	100 *	
126	1320	127 *	
126	1330	150	194
126	1340	181 *	
126	1350	221 *	
126	1400	240	254
126	1410	270 *	
126	1420	293	
126	1430	310	151
126	1440	321	
126	1450	328	
126	1500	336	72
126	1510	340 *	
126	1520	340	
126	1530	340 *	1
126	1540	340	
126	1550	341 *	
126	1600	341 *	0
126	1610	340	
126	1620	340	
126	1630	340	0
126	1700	340	0
126	1730	341	0
126	1800	341	0
127	600	300 *	0
127	630	300 *	0
127	700	300	1
127	730	300 *	
127	800	300	
127	830	300	6
127	900	300	10
127	930	300	18
127	940	300	
127	950	300	
127	1000	300	22
127	1010	300 *	
127	1020	300	
127	1030	290 *	30
127	1040	256	
127	1050	196	
127	1100	110	98
127	1110	65 *	
127	1120	45 *	
127	1130	36	93

Day of Year	Time	Sandy	Rocky	Day of Year	Time	Sandy	Rocky
127	1140	29 *		128	950	232 *	
127	1150	18 *		128	1000	174	174
127	1200	13 *	57	128	1010	119	
127	1210	14		128	1020	89 *	
127	1220	13		128	1030	75 *	95
127	1230	11	63	128	1040	71 *	
127	1240	19		128	1050	63 *	
127	1250	17		128	1100	55 *	84
127	1300	25	86	128	1110	47	
127	1310	39 *		128	1120	33	
127	1320	63		128	1130	27 *	64
127	1330	79	131	128	1140	22 *	
127	1340	123		128	1150	13	
127	1350	145 *		128	1200	5	44
127	1400	178 *	197	128	1210	1	
127	1410	199 *		128	1220	0 *	
127	1420	219		128	1230	4	58
127	1430	233	257	128	1240	10 *	
127	1440	249		128	1250	17	
127	1450	266		128	1300	32	93
127	1500	278	271	128	1310	54 *	
127	1510	288 *		128	1320	70 *	
127	1520	298		128	1330	95	178
127	1530	305 *	228	128	1340	115	
127	1540	309 *		128	1350	134	
127	1550	310 *		128	1400	159 *	207
127	1600	312 *	116	128	1410	171 *	
127	1610	312		128	1420	196 *	
127	1620	313		128	1430	218 *	246
127	1630	313	175	128	1440	236 *	
127	1700	313 *	143	128	1450	248 *	
127	1730	312 *	176	128	1500	254	295
127	1800	312 *	126	128	1510	258	
128	700	335 *	130	128	1520	264	
128	730	335	146	128	1530	270	283
128	800	335	158	128	1540	272 *	
128	830	335 *	176	128	1550	273	
128	840	335		128	1600	276	298
128	850	334		128	1630	279	293
128	900	332 *	185	128	1700	281 *	287
128	910	330 *		128	1730	281	243
128	920	316 *		129	700	334	202
128	930	303 *	224	129	730	334	240
128	940	271 *		129	800	334	252

Day of Year	Time	Sandy	Rocky	Day of Year	Time	Sandy	Rocky
129	830	334 *	255	129	1730	261 *	186
129	840	334 *		130	700	313	257
129	850	333 *		130	730	313 *	279
129	900	333	276	130	800	313 *	297
129	910	333 *		130	830	313 *	317
129	920	327 *		130	840	313	
129	930	319	305	130	850	313	
129	940	293		130	900	313	358
129	950	261 *		130	910	313	
129	1000	227 *	248	130	920	313 *	
129	1010	206		130	930	313 *	348
129	1020	169 *		130	940	313 *	
129	1030	138	176	130	950	313 *	
129	1040	116		130	1000	313	359
129	1050	78		130	1010	313	
129	1100	62 *	72	130	1020	313 *	
129	1110	45 *		130	1030	313	341
129	1120	32 *		130	1040	313	
129	1130	21	36	130	1050	312	
129	1140	10		130	1100	310 *	345
129	1150	8 *		130	1110	304	
129	1200	7 *	42	130	1120	297 *	
129	1210	7		130	1130	282	314
129	1220	0 *		130	1140	181	
129	1230	2 *	45	130	1150	85 *	
129	1240	9 *		130	1200	35	171
129	1250	17 *		130	1210	22	
129	1300	28	76	130	1220	16	
129	1310	44 *		130	1230	15 *	103
129	1320	59		130	1240	12	
129	1330	71 *	154	130	1250	14 *	
129	1340	95		130	1300	15	131
129	1350	118 *		130	1310	23	
129	1400	138	251	130	1320	38	
129	1410	159 *		130	1330	55	146
129	1420	174		130	1340	84	
129	1430	194	307	130	1350	114 *	
129	1440	213 *		130	1400	152 *	261
129	1450	228		130	1410	185	
129	1500	235 *	355	130	1420	213 *	
129	1530	250 *	378	130	1430	237	282
129	1600	257 *	312	130	1440	257	
129	1630	260	287	130	1450	272 *	
129	1700	260 *	239	130	1500	276 *	311

Day of Year	Time	Sandy	Rocky	Day of Year	Time	Sandy	Rocky
130	1530	291 *	325	131	1430	163	226
130	1600	294 *	325	131	1440	189 *	
130	1630	292	340	131	1450	205 *	
130	1700	293 *	276	131	1500	224	305
130	1730	296	335	131	1510	242 *	
131	700	355	293	131	1520	260	
131	730	355	296	131	1530	279 *	340
131	800	355 *	307	131	1600	297	352
131	830	355 *	286	131	1630	298	373
131	840	355 *		131	1700	303 *	292
131	850	355 *		131	1730	306	302
131	900	355	367	132	700	289	277
131	910	355 *		132	730	289	306
131	920	355		132	800	289	251
131	930	355	327	132	830	289	314
131	940	355		132	840	289	
131	950	355		132	850	289 *	
131	1000	354	358	132	900	285 *	329
131	1010	353		132	910	277	
131	1020	343 *		132	920	262 *	
131	1030	333	299	132	930	246 *	311
131	1040	327		132	940	205 *	
131	1050	320 *		132	950	166 *	
131	1100	314 *	282	132	1000	145 *	361
131	1110	305		132	1010	119 *	
131	1120	288		132	1020	98	
131	1130	275	319	132	1030	79 *	306
131	1140	241		132	1040	64	
131	1150	166		132	1050	52	
131	1200	116	300	132	1100	47 *	211
131	1210	96 *		132	1110	37 *	
131	1220	80 *		132	1120	28	
131	1230	67 *	209	132	1130	16	160
131	1240	55 *		132	1140	14	
131	1250	37 *		132	1150	13	
131	1300	34 *	150	132	1200	8 *	152
131	1310	34		132	1210	6	
131	1320	43 *		132	1220	1	
131	1330	46 *	120	132	1230	2	152
131	1340	60		132	1240	0 *	
131	1350	81 *		132	1250	8 *	
131	1400	102		132	1300	16 *	163
131	1410	118 *		132	1310	18 *	
131	1420	147		132	1320	26	

Day of Year	Time	Sandy	Rocky	Day of Year	Time	Sandy	Rocky
132	1330	34 *	194	133	1150	14 *	
132	1340	51		133	1200	9 *	172
132	1350	63 *		133	1210	11 *	
132	1400	75	234	133	1220	13 *	
132	1410	98 *		133	1230	0 *	161
132	1420	116 *		133	1240	1	
132	1430	136	312	133	1250	10	
132	1440	149 *		133	1300	16	200
132	1450	158 *		133	1310	23 *	
132	1500	173	369	133	1320	39	
132	1510	183		133	1330	55 *	362
132	1520	189		133	1340	58	
132	1530	196	379	133	1350	71	
132	1540	200		133	1400	83 *	341
132	1550	204		133	1410	99 *	
132	1600	204 *	396	133	1420	110	
132	1610	206		133	1430	129	385
132	1620	207		133	1440	136 *	
132	1630	210	378	133	1450	142	
132	1640	210 *		133	1500	151	398
132	1650	210		133	1510	156	
132	1700	210 *	367	133	1520	161 *	
132	1710	210		133	1530	163 *	391
132	1720	210		133	1540	162	
132	1730	210	320	133	1550	165 *	
133	700	216 *	318	133	1600	166	389
133	730	216 *	305	133	1610	166	
133	800	216 *	296	133	1630	165	435
133	830	216	309	133	1700	165	393
133	900	216 *	327	133	1730	165 *	297
133	930	216	342	134	700	196 *	355
133	940	216		134	730	196 *	363
133	950	216		134	800	196 *	371
133	1000	216	325	134	830	196 *	358
133	1010	214		134	840	196	
133	1020	200 *		134	850	196 *	
133	1030	165	354	134	900	196	366
133	1040	130		134	910	196 *	
133	1050	82 *		134	920	196 *	
133	1100	62 *	252	134	930	196	358
133	1110	47		134	940	196	
133	1120	38		134	950	196	
133	1130	30	158	134	1000	196 *	356
133	1140	20 *		134	1010	196 *	

Day of Year	Time	Sandy	Rocky		Day of Year	Time	Sandy	Rocky
134	1020	196			135	900	150 *	358
134	1030	196	364		135	910	149	
134	1040	196			135	920	149	
134	1050	196 *			135	930	144	357
134	1100	190	355		135	940	134	
134	1110	175 *			135	950	128	
134	1120	146 *			135	1000	109	359
134	1130	129 *	346		135	1010	76 *	
134	1140	114			135	1020	56	
134	1150	107			135	1030	34	174
134	1200	94	312		135	1040	25	
134	1210	73			135	1050	21	
134	1220	43			135	1100	20 *	142
134	1230	29	259		135	1110	17	
134	1240	17			135	1120	13 *	
134	1250	12 *			135	1130	8	171
134	1300	9 *	151		135	1140	5	
134	1310	12 *			135	1150	4 *	
134	1320	13			135	1200	2	183
134	1330	19 *	140		135	1210	0 *	
134	1340	28			135	1220	1 *	
134	1350	32			135	1230	0	
134	1400	51	216		135	1240	3 *	
134	1410	63 *			135	1250	10 *	
134	1420	82			135	1300	9 *	237
134	1430	92 *	268		135	1310	13	
134	1440	104 *			135	1320	16	
134	1450	114			135	1330	22 *	253
134	1500	127			135	1340	27	
134	1510	131			135	1350	30	
134	1520	141 *			135	1400	34	304
134	1530	150			135	1410	45	
134	1540	155			135	1420	51 *	
134	1550	158 *			135	1430	53 *	338
134	1600	162			135	1440	59	
134	1630	167 *			135	1450	67 *	
134	1700	167			135	1500	75	355
134	1730	167			135	1510	80 *	
135	700	150			135	1520	85 *	
135	730	150	289		135	1530	88 *	352
135	800	150 *	361		135	1540	89 *	
135	830	150	369		135	1550	91 *	
135	840	150			135	1600	92 *	322
135	850	150 *			135	1630	92 *	404

Day of Year	Time	Sandy	Rocky
135	1700	92 *	398
135	1730	92 *	352
136	700	104 *	210
136	730	104 *	312
136	800	103	368
136	830	99 *	376
136	900	90	363
136	920	75	
136	930	57 *	334
136	940	48 *	
136	950	34	
136	1000	28 *	280
136	1010	18	
136	1020	7 *	
136	1030	8	191
136	1040	7	
136	1050	8	
136	1100	7 *	207
136	1110	9 *	
136	1120	8 *	
136	1130	3 *	136
136	1140	5 *	
136	1150	8	
136	1200	6	166
136	1210	5 *	
136	1220	8	
136	1230	10	185
136	1240	10	
136	1250	10 *	
136	1300	9 *	249
136	1310	11	
136	1320	12 *	
136	1330	15 *	281
136	1340	21 *	
136	1350	23 *	
136	1400	29	308
136	1410	35	
136	1420	38 *	
136	1430	42 *	327
136	1440	48 *	
136	1450	52 *	
136	1500	54	294
136	1510	60 *	
136	1520	62	

Day of Year	Time	Sandy	Rocky
136	1530	63	271
136	1540	66 *	
136	1550	67 *	
136	1600	68 *	249
136	1610	68 *	
136	1620	68 *	
136	1630	68 *	314
136	1700	70 *	
136	1730	70 *	272

Table A- 3. Rocky Site Photographs Lost. Counts for the Rocky site could not be generated at these times.

Date	Time
30 April 2011	1630
	1700
4 May 2011	900
	1430
	1500
7 May 2011	730
	800
11 May 2011	1400
14 May 2011	1500
	1600
	1630
	1700
	1730
15 May 2011	700
	1230
16 May 2011	1700

Table A- 4. Entire Data Set for Environmental Variables. Abbreviations are those given in Table 1. DOY represents day of year, with day 120 equivalent to 30 April. Dashed lines separate each day.

DoY	$H_r(t)$	$S_r(t)$	$S_e(t)$	$T(t)$	$S_p(t)$	$A(t)$	$H_u(t)$	$D(t)$	$W_s(t)$	$W_d(t)$	$W_c(t)$	$H_x(t)$	$T_x(t)$	$B(t)$
120	6	3.6	-0.898	0.563	24.36	25.1	90	23.4	0	112.5	25.1	27.4	27.4	756.1
120	6.5	18.4	6.333	0.588	24.35	25.9	87	23.6	0	112.5	25.9	28.7	28.7	756.4
120	7	134.2	13.54	0.617	24.34	26.6	85	23.9	1.6	67.5	26.6	29.7	29.7	756.6
120	7.5	250	20.7	0.658	24.39	27.2	83	24	6.4	67.5	27.2	30.6	30.6	756.8
120	8	300	27.82	0.744	24.44	27.6	82	24.3	3.2	67.5	27.6	31.6	31.6	757.3
120	8.5	426	34.85	0.842	24.38	27.6	85	24.8	4.8	45	27.6	31.9	31.9	757.6
120	9	550	41.76	0.945	24.32	27.7	87	25.3	4.8	67.5	27.7	32.5	32.5	757.5
120	9.5	730	48.42	1.047	24.34	29.5	76	24.8	4.8	315	29.5	35.1	35.1	757.5
120	10	785	54.6	1.141	24.36	29.7	73	24.4	8	225	29.7	35.1	35.1	757.4
120	10.5	880	59.99	1.25	24.36	30.5	68	23.9	12.9	225	30.4	35.8	35.8	757.5
120	11	900	64.24	1.363	24.36	30.2	71	24.3	14.5	225	29.9	35.7	35.4	757
120	11.5	1040	67.01	1.464	24.54	30.3	68	23.8	14.5	225	30.1	35.5	35.3	756.7
120	12	760	68.11	1.548	24.73	29.9	71	24.1	16.1	225	29.5	35.2	34.8	756.3
120	12.5	940	67.46	1.592	24.63	30.2	72	24.6	17.7	225	29.7	36.1	35.6	755.9
120	13	910	65.1	1.603	24.53	30.8	69	24.5	19.3	225	30.3	36.6	36.1	755.4
120	13.5	860	61.19	1.577	24.62	30.3	73	24.9	20.9	225	29.6	36.4	35.7	755.1
120	14	830	56.05	1.517	24.7	30.3	72	24.7	19.3	225	29.7	36.2	35.6	754.9
120	14.5	830	50.04	1.432	24.55	30.1	73	24.7	17.7	225	29.6	36	35.4	754.7
120	15	650	43.47	1.331	24.39	30.2	73	24.8	19.3	225	29.6	36.2	35.6	754.5
120	15.5	550	36.62	1.209	24.42	30.3	72	24.7	19.3	225	29.7	36.3	35.7	754.3
120	16	590	29.62	1.077	24.46	29.8	73	24.4	17.7	225	29.2	35.2	34.6	754.3
120	16.5	160	22.53	0.938	24.5	29	75	24.1	17.7	225	28.3	33.9	33.2	754.3
120	17	135	15.38	0.814	24.53	29.2	74	24.1	16.1	202.5	28.6	34.1	33.5	754.5
120	17.5	55	8.181	0.693	24.48	28.1	77	23.7	14.5	202.5	27.7	32.1	31.6	754.7
120	18	13	0.962	0.576	24.44	27.3	80	23.6	14.5	202.5	26.8	30.6	30	755

DoY	$H_r(t)$	$S_r(t)$	$S_e(t)$	$T(t)$	$S_p(t)$	$A(t)$	$H_u(t)$	$D(t)$	$W_s(t)$	$W_d(t)$	$W_c(t)$	$H_x(t)$	$T_x(t)$	$B(t)$
121	6	4	-0.866	0.64	24.48	25.6	89	23.6	1.6	225	25.6	28.2	28.2	755.7
121	6.5	33	6.353	0.623	24.44	25.7	88	23.6	1.6	90	25.7	28.4	28.4	756.1
121	7	130	13.55	0.611	24.39	26.8	83	23.7	1.6	202.5	26.8	29.9	29.9	756.5
121	7.5	230	20.7	0.606	24.39	27.3	83	24.2	4.8	247.5	27.3	31	31	756.3
121	8	335	27.79	0.63	24.39	28.7	76	24	9.7	225	28.7	33.3	33.3	756.7
121	8.5	175	34.81	0.677	24.36	29.3	71	23.5	12.9	225	29.2	33.7	33.6	756.9
121	9	635	41.69	0.739	24.34	27.4	83	24.2	12.9	90	27.2	31.1	30.9	757.2
121	9.5	730	48.33	0.831	24.29	26.5	86	24	14.5	67.5	25.9	29.6	29	757.3
121	10	890	54.48	0.955	24.24	27.1	84	24.1	9.7	67.5	27.1	30.5	30.5	757.3
121	10.5	910	59.84	1.093	24.33	29.4	74	24.3	4.8	45	29.4	34.5	34.5	756.6
121	11	860	64.05	1.226	24.41	30.7	69	24.3	16.1	225	30.3	36.3	36	756.3
121	11.5	948	66.8	1.346	24	30.3	69	24	19.3	225	29.7	35.6	34.9	756
121	12	997	67.89	1.441	23.59	30.4	70	24.4	20.9	225	29.8	36.2	35.5	755.4
121	12.5	1180	67.23	1.52	23.56	30.1	72	24.5	22.5	225	29.3	35.8	35	755.4
121	13	900	64.88	1.581	23.52	30.3	73	24.9	20.9	225	29.6	36.6	35.8	755.4
121	13.5	600	60.99	1.622	23.5	30.2	72	24.6	20.9	225	29.4	35.9	35.2	755
121	14	450	55.88	1.623	23.47	30.1	72	24.5	19.3	225	29.4	35.7	35	754.5
121	14.5	310	49.89	1.569	23.69	29.1	75	24.2	16.1	225	28.6	34.2	33.6	754.3
121	15	69	43.35	1.462	23.91	28.1	78	23.9	12.9	90	27.9	32.1	31.9	753.9
121	15.5	30	36.52	1.336	23.73	27.3	82	23.9	8	202.5	27.3	30.7	30.7	754.2
121	16	77	29.53	1.206	23.55	26.2	89	24.2	3.2	202.5	26.2	29.3	29.3	754
121	16.5	130	22.46	1.075	23.64	25.2	92	23.8	3.2	45	25.2	27.7	27.7	753.9
121	17	111	15.33	0.927	23.74	25.9	90	24.1	3.2	67.5	25.9	28.8	28.8	753.7
121	17.5	14	8.142	0.779	23.85	25.8	90	24	1.6	22.5	25.8	28.7	28.7	754.1
121	18	2	0.935	0.628	23.95	25.4	93	24.2	1.6	22.5	25.4	28.1	28.1	754.6
122	6	4	-0.833	0.748	22.32	24.1	96	23.4	0	247.5	24.1	26.2	26.2	755.4
122	6.5	27	6.374	0.688	22.32	24.4	97	23.9	1.6	45	24.4	26.7	26.7	755.5

DoY	$H_r(t)$	$S_r(t)$	$S_e(t)$	$T(t)$	$S_p(t)$	$A(t)$	$H_u(t)$	$D(t)$	$W_s(t)$	$W_d(t)$	$W_c(t)$	$H_x(t)$	$T_x(t)$	$B(t)$
122	7	43	13.55	0.634	22.32	25.1	94	24	1.6	90	25.1	27.6	27.6	755.6
122	7.5	165	20.69	0.591	22.39	25.4	93	24.2	3.2	67.5	25.4	28.2	28.2	756.2
122	8	350	27.77	0.587	22.47	26.5	90	24.7	1.6	45	26.5	30.1	30.1	756.4
122	8.5	460	34.77	0.605	23.38	27.4	86	24.9	1.6	45	27.4	31.7	31.7	756.7
122	9	560	41.63	0.644	24.29	27.4	86	24.8	3.2	292.5	27.4	31.6	31.6	756.8
122	9.5	730	48.24	0.713	24.25	28.1	85	25.3	3.2	270	28.1	33.2	33.2	756.6
122	10	790	54.36	0.822	24.2	27.8	85	25	6.4	270	27.8	32.4	32.4	756.5
122	10.5	410	59.68	0.954	23.85	28.6	81	25	4.8	270	28.6	34.1	34.1	756.4
122	11	430	63.87	1.095	23.5	28.3	82	25	4.8	270	28.3	33.5	33.5	756.2
122	11.5	330	66.59	1.231	23.7	28.3	82	24.9	4.8	270	28.3	33.3	33.3	756.2
122	12	130	67.67	1.353	23.91	27.5	86	24.9	8	247.5	27.5	31.9	31.9	755.7
122	12.5	1155	67.01	1.463	23.28	29.3	78	25	8	270	29.3	35.1	35.1	755.6
122	13	397	64.67	1.566	22.66	28.3	81	24.7	12.9	247.5	28.1	33.2	33	755.1
122	13.5	700	60.79	1.642	22.55	28.9	79	24.9	12.9	225	28.8	34.6	34.4	754.8
122	14	147	55.71	1.676	22.44	27.4	88	25.3	14.5	225	26.9	32.1	31.6	754.2
122	14.5	134	49.75	1.669	22.6	27.1	87	24.7	12.9	225	26.8	30.9	30.7	754.4
122	15	143	43.23	1.573	22.75	25.8	94	24.8	11.3	202.5	25.8	29.1	29.1	754.8
122	15.5	130	36.42	1.428	22.63	25.8	94	24.8	9.7	225	25.8	29.1	29.1	754.1
122	16	111	29.45	1.284	22.51	25.8	95	25	9.7	202.5	25.8	29.2	29.2	754
122	16.5	89	22.4	1.123	22.51	25.8	95	25	9.7	202.5	25.8	29.2	29.2	754
122	17	72	15.27	1.013	22.51	25.9	94	24.9	9.7	225	25.9	29.4	29.4	754.2
122	17.5	24	8.101	0.903	22.44	25.6	95	24.8	9.7	202.5	25.6	28.7	28.7	754.3
122	18	1	0.905	0.792	22.37	25.5	95	24.6	8	202.5	25.5	28.4	28.4	754.5
123	6	3	-0.81	0.925	21.94	23.8	97	23.3	0	90	23.8	25.8	25.8	756.2
123	6.5	75	6.387	0.828	21.92	24.5	96	23.8	1.6	45	24.5	26.8	26.8	756.4
123	7	140	13.56	0.734	21.89	25.3	93	24.1	0	67.5	25.3	27.9	27.9	756.8
123	7.5	115	20.68	0.65	22.05	24.7	95	23.8	3.2	67.5	24.7	27	27	757.4

DoY	$H_r(t)$	$S_r(t)$	$S_e(t)$	$T(t)$	$S_p(t)$	$A(t)$	$H_u(t)$	$D(t)$	$W_s(t)$	$W_d(t)$	$W_c(t)$	$H_x(t)$	$T_x(t)$	$B(t)$
123	8	490	27.75	0.605	22.2	26.1	94	25.1	0	67.5	26.1	29.8	29.8	757.6
123	8.5	415	34.73	0.589	22.43	26.2	94	25.2	3.2	270	26.2	30	30	757.8
123	9	662	41.57	0.603	22.66	26.6	92	25.2	4.8	247.5	26.6	30.6	30.6	757.9
123	9.5	690	48.15	0.647	22.54	27.1	90	25.3	4.8	247.5	27.1	31.4	31.4	757.9
123	10	730	54.24	0.723	22.42	27.3	90	25.5	6.4	247.5	27.3	32.1	32.1	757.8
123	10.5	825	59.53	0.827	22.38	27.7	88	25.5	4.8	247.5	27.7	32.7	32.7	757.7
123	11	860	63.69	0.957	22.35	28.2	85	25.4	6.4	247.5	28.2	33.5	33.5	757.5
123	11.5	920	66.39	1.099	22.35	28.2	87	25.8	8	247.5	28.2	33.9	33.9	757.1
123	12	930	67.46	1.236	22.35	28.4	85	25.6	6.4	247.5	28.4	34.1	34.1	756.9
123	12.5	990	66.79	1.371	22.39	28.5	82	25.1	8	247.5	28.5	33.9	33.9	756.6
123	13	975	64.46	1.508	22.44	28.5	82	25.1	6.4	247.5	28.5	33.9	33.9	756.3
123	13.5	895	60.6	1.628	22.45	28.6	81	25	8	247.5	28.6	34.1	34.1	756
123	14	720	55.54	1.706	22.47	28.4	80	24.6	8	247.5	28.4	33.3	33.3	755.6
123	14.5	649	49.61	1.735	22.5	29.1	78	24.8	6.4	247.5	29.1	34.7	34.7	755.4
123	15	345	43.12	1.709	22.54	28.8	80	25	8	247.5	28.8	34.6	34.6	755.2
123	15.5	500	36.33	1.656	22.54	28.6	80	24.8	8	247.5	28.6	33.9	33.9	755
123	16	370	29.37	1.575	22.54	28.4	80	24.6	8	247.5	28.4	33.3	33.3	754.9
123	16.5	190	22.33	1.462	22.54	27.3	85	24.6	9.7	247.5	27.3	31.3	31.3	755
123	17	160	15.22	1.314	22.54	27.3	86	24.7	8	247.5	27.3	31.3	31.3	755.2
123	17.5	85	8.06	1.164	22.53	26.7	89	24.7	6.4	247.5	26.7	30.3	30.3	755.5
123	18	11	0.875	1.01	22.51	25.8	92	24.4	6.4	247.5	25.8	28.9	28.9	755.7
124	6	3	-0.778	1.139	22.97	23.3	99	23.1	1.6	112.5	23.3	25.2	25.2	756.6
124	6.5	35	6.407	1.019	22.78	23.8	98	23.5	1.6	22.5	23.8	25.9	25.9	756.9
124	7	110	13.56	0.901	22.59	24.2	97	23.7	1.6	67.5	24.2	26.3	26.3	757.4
124	7.5	160	20.67	0.786	22.73	24.7	94	23.7	1.6	45	24.7	27.1	27.1	757.6
124	8	260	27.72	0.684	22.87	24.9	95	24	3.2	45	24.9	27.3	27.3	757.8
124	8.5	410	34.69	0.596	23.14	25.6	93	24.4	3.2	67.5	25.6	28.6	28.6	757.9

DoY	$H_r(t)$	$S_r(t)$	$S_e(t)$	$T(t)$	$S_p(t)$	$A(t)$	$H_u(t)$	$D(t)$	$W_s(t)$	$W_d(t)$	$W_c(t)$	$H_x(t)$	$T_x(t)$	$B(t)$
124	9	540	41.51	0.543	23.4	26.9	89	25	1.6	45	26.9	30.9	30.9	758
124	9.5	690	48.06	0.539	23.27	27.7	85	25	1.6	315	27.7	32.3	32.3	758.1
124	10	715	54.11	0.583	23.14	27.5	85	24.8	3.2	247.5	27.5	31.7	31.7	758.2
124	10.5	800	59.38	0.671	23.18	27.9	83	24.8	4.8	270	27.9	32.6	32.6	758.3
124	11	880	63.51	0.78	23.23	28.4	81	24.8	4.8	292.5	28.4	33.5	33.5	758.2
124	11.5	935	66.19	0.907	23.56	28.7	80	24.9	6.4	270	28.7	34.3	34.3	757.8
124	12	900	67.24	1.056	23.88	29.8	73	24.5	11.3	247.5	29.8	35.3	35.3	757.4
124	12.5	910	66.57	1.213	23.33	29.8	72	24.2	14.5	225	29.6	35.2	34.9	756.9
124	13	895	64.25	1.36	22.78	28.6	79	24.6	11.3	247.5	28.6	33.6	33.6	756.4
124	13.5	855	60.41	1.49	22.8	29.2	74	24.1	14.5	225	28.9	34.2	33.8	756
124	14	595	55.38	1.592	22.82	29.2	76	24.6	14.5	225	28.9	34.6	34.2	755.9
124	14.5	580	49.47	1.664	22.86	28.9	78	24.7	16.1	225	28.3	34.4	33.8	755.7
124	15	400	43	1.707	22.9	29.1	79	25.1	14.5	225	28.7	34.9	34.6	755.5
124	15.5	585	36.23	1.704	22.88	29.3	79	25.3	14.5	225	28.9	35.3	34.9	755.3
124	16	468	29.3	1.663	22.87	29.2	79	25.1	14.5	202.5	28.8	35.1	34.7	755
124	16.5	250	22.27	1.585	22.92	28.8	80	25	14.5	202.5	28.4	34.6	34.2	755
124	17	220	15.17	1.463	22.97	28	83	24.8	14.5	225	27.5	32.7	32.2	755
124	17.5	50	8.024	1.338	22.96	27.6	85	24.9	14.5	225	27.1	32	31.5	755.3
124	18	11	0.851	1.209	22.94	26.9	87	24.6	12.9	225	26.7	30.7	30.4	755.7
125	6	1.4	-0.758	1.344	23.14	23.9	97	23.4	0	213.75	23.9	25.9	25.9	757.4
125	6.5	18.5	6.417	1.179	23.14	24.3	96	23.7	0	202.5	24.3	26.6	26.6	757.5
125	7	77	13.56	1.015	23.14	24.7	95	23.8	1.6	225	24.7	27	27	757.8
125	7.5	225	20.66	0.863	23.04	25.3	93	24.1	1.6	315	25.3	28	28	757.9
125	8	415	27.69	0.743	22.94	26.2	90	24.5	1.6	22.5	26.2	29.5	29.5	758.2
125	8.5	250	34.64	0.643	23.29	25.3	92	23.9	3.2	22.5	25.3	27.8	27.8	758.1
125	9	350	41.44	0.565	23.64	25.7	91	24.1	1.6	45	25.7	28.6	28.6	758.2
125	9.5	405	47.97	0.508	23.76	26.6	88	24.4	3.2	45	26.6	29.9	29.9	758.2

DoY	$H_r(t)$	$S_r(t)$	$S_e(t)$	$T(t)$	$S_p(t)$	$A(t)$	$H_u(t)$	$D(t)$	$W_s(t)$	$W_d(t)$	$W_c(t)$	$H_x(t)$	$T_x(t)$	$B(t)$
125	10	750	53.99	0.497	23.88	27.4	84	24.4	4.8	270	27.4	31.3	31.3	758.2
125	10.5	530	59.22	0.549	23.42	29.3	74	24.2	9.7	225	29.3	34.3	34.3	758.2
125	11	1230	63.33	0.643	22.97	29.3	76	24.6	14.5	225	28.9	34.7	34.3	758.1
125	11.5	850	65.98	0.764	22.91	28.4	80	24.7	14.5	225	28	33.5	33.1	757.9
125	12	1120	67.03	0.886	22.85	28.9	78	24.7	16.1	225	28.3	34.3	33.7	757.6
125	12.5	915	66.36	1.012	22.72	30	73	24.6	17.7	225	29.4	35.7	35.2	756.9
125	13	945	64.04	1.143	22.59	30	76	25.3	17.7	225	29.4	36.3	35.8	756.7
125	13.5	855	60.23	1.279	22.55	29.9	77	25.4	19.3	225	29.2	36.2	35.6	756.3
125	14	790	55.21	1.41	22.51	29.7	77	25.2	17.7	202.5	29.1	35.7	35.1	755.9
125	14.5	780	49.33	1.519	22.5	29.4	78	25.1	19.3	202.5	28.6	35.3	34.5	755.8
125	15	215	42.89	1.6	22.49	28.4	81	24.9	17.7	202.5	27.6	33.6	32.8	755.6
125	15.5	215	36.14	1.636	22.48	27.4	85	24.7	16.1	225	26.6	31.6	30.7	755.6
125	16	205	29.22	1.635	22.47	27.6	85	24.8	16.1	225	26.8	31.9	31.1	755.6
125	16.5	7	22.21	1.599	22.55	27.1	88	25	14.5	202.5	26.6	31.2	30.7	755.6
125	17	44	15.13	1.516	22.63	26.1	93	24.8	11.3	202.5	26.1	29.5	29.5	755.9
125	17.5	35	7.992	1.428	22.62	25.7	94	24.7	9.7	202.5	25.7	28.9	28.9	756.4
125	18	4	0.83	1.336	22.61	25.6	94	24.6	6.4	202.5	25.6	28.6	28.6	756.4
126	6	5	-0.738	1.43	22.85	23.7	98	23.3	1.6	67.5	23.7	25.7	25.7	757.6
126	6.5	23	6.425	1.312	22.87	23.9	97	23.4	0	112.5	23.9	26.1	26.1	757.7
126	7	120	13.56	1.19	22.9	25.4	92	24	0	236.25	25.4	28.1	28.1	758
126	7.5	215	20.64	1.07	22.9	27.1	85	24.3	0	360	27.1	30.6	30.6	758.3
126	8	360	27.66	0.947	22.9	26.8	88	24.7	1.6	315	26.8	30.6	30.6	758.6
126	8.5	270	34.59	0.842	22.85	26.6	88	24.4	1.6	45	26.6	29.9	29.9	758.6
126	9	556	41.37	0.761	22.8	27.3	84	24.4	3.2	22.5	27.3	31.2	31.2	758.5
126	9.5	630	47.87	0.686	22.73	27.2	85	24.5	8	247.5	27.2	31	31	758.5
126	10	710	53.86	0.631	22.66	28.9	78	24.7	9.7	225	28.9	34.3	34.3	758.1
126	10.5	770	59.07	0.621	22.62	29.2	78	25	16.1	202.5	28.7	34.9	34.4	757.8

DoY	$H_r(t)$	$S_r(t)$	$S_e(t)$	$T(t)$	$S_p(t)$	$A(t)$	$H_u(t)$	$D(t)$	$W_s(t)$	$W_d(t)$	$W_c(t)$	$H_x(t)$	$T_x(t)$	$B(t)$
126	11	860	63.14	0.649	22.59	28.8	80	25	17.7	225	28.1	34.6	33.8	757.5
126	11.5	915	65.78	0.698	22.56	28.1	83	24.9	17.7	225	27.2	32.9	32	756.9
126	12	915	66.81	0.763	22.54	28.9	82	25.5	19.3	225	28	35.1	34.2	756.8
126	12.5	975	66.15	0.861	22.48	29.2	80	25.4	20.9	202.5	28.2	35.2	34.3	756.5
126	13	220	63.84	0.989	22.42	28.8	82	25.4	20.9	225	27.8	34.8	33.8	756.3
126	13.5	950	60.05	1.133	22.45	29.1	79	25.1	20.9	202.5	28.2	34.9	34	756
126	14	340	55.06	1.27	22.49	29.2	78	24.9	19.3	202.5	28.3	34.8	34	755.9
126	14.5	840	49.2	1.393	22.3	29	79	25	16.1	202.5	28.4	34.7	34.1	755.5
126	15	220	42.78	1.502	22.11	28.6	81	25	16.1	202.5	28	34.1	33.5	755.2
126	15.5	500	36.06	1.593	22.16	28.8	80	25	16.1	202.5	28.2	34.6	33.9	754.8
126	16	320	29.16	1.642	22.2	28.9	79	24.9	17.7	202.5	28.2	34.5	33.8	754.7
126	16.5	350	22.16	1.653	22.08	28.9	80	25.1	16.1	202.5	28.3	34.7	34.1	754.6
126	17	75	15.09	1.609	21.96	27.6	83	24.5	16.1	202.5	26.8	31.7	30.9	754.7
126	17.5	80	7.962	1.557	22.15	26.9	87	24.5	14.5	202.5	26.3	30.6	29.9	754.9
126	18	5	0.811	1.502	22.34	26.3	89	24.3	11.3	202.5	26.3	29.5	29.5	755.4
127	6	3	-0.716	1.644	21.46	24.7	94	23.6	8	180	24.7	26.9	26.9	756.6
127	6.5	18	6.435	1.511	21.46	24.6	94	23.5	8	202.5	24.6	26.8	26.8	756.7
127	7	336	13.55	1.377	21.46	25.4	89	23.4	3.2	112.5	25.4	27.8	27.8	757.1
127	7.5	82	20.62	1.245	21.47	24.8	91	23.3	1.6	67.5	24.8	27	27	757.5
127	8	133	27.63	1.119	21.49	26.3	86	23.8	4.8	180	26.3	29.3	29.3	757.5
127	8.5	182	34.54	0.995	21.44	26.6	86	24.1	14.5	202.5	26	29.8	29.2	757.6
127	9	262	41.29	0.889	21.39	27.2	83	24.1	12.9	202.5	27	30.7	30.5	757.6
127	9.5	283	47.77	0.809	22.37	28	80	24.2	14.5	202.5	27.5	32.2	31.7	757.5
127	10	456	53.74	0.739	21.56	28.4	78	24.2	14.5	180	28	33.1	32.7	757.3
127	10.5	750	58.91	0.684	21.56	29.4	75	24.5	17.7	180	28.8	34.8	34.1	757.1
127	11	1080	62.96	0.645	21.56	30.2	72	24.6	19.3	180	29.6	35.9	35.3	757
127	11.5	890	65.58	0.638	21.62	29.9	74	24.8	20.9	157.5	29.2	35.8	35	756.9

DoY	$H_r(t)$	$S_r(t)$	$S_e(t)$	$T(t)$	$S_p(t)$	$A(t)$	$H_u(t)$	$D(t)$	$W_s(t)$	$W_d(t)$	$W_c(t)$	$H_x(t)$	$T_x(t)$	$B(t)$
127	12	971	66.61	0.669	21.68	29.8	72	24.2	20.9	180	28.9	35	34.2	756.7
127	12.5	920	65.94	0.731	21.76	30.1	70	24	20.9	180	29.3	35.3	34.5	756.4
127	13	920	63.64	0.824	21.84	30.4	71	24.5	22.5	180	29.6	36.2	35.4	756.1
127	13.5	1070	59.86	0.941	21.77	29.8	73	24.4	22.5	180	28.8	35.2	34.3	755.9
127	14	870	54.9	1.068	21.7	29.8	72	24.2	22.5	180	28.8	35	34.1	755.7
127	14.5	382	49.07	1.196	21.75	30.5	70	24.4	20.9	180	29.8	36.3	35.6	755.7
127	15	428	42.67	1.324	21.8	28.6	78	24.3	22.5	202.5	27.4	33.4	32.2	755.8
127	15.5	187	35.97	1.449	21.77	28.2	77	23.8	22.5	180	26.9	32.2	30.9	755.1
127	16	143	29.09	1.556	21.75	27.4	81	23.8	20.9	180	26.1	30.8	29.6	755.1
127	16.5	85	22.1	1.62	21.78	27.2	82	23.9	20.9	202.5	25.9	30.6	29.2	755.2
127	17	51	15.04	1.626	21.82	26.7	83	23.5	19.3	180	25.4	29.6	28.3	755.5
127	17.5	24	7.932	1.625	21.82	26.4	83	23.3	19.3	180	25.1	29.1	27.8	755.7
127	18	3	0.793	1.62	21.82	25.9	86	23.4	17.7	180	24.7	28.4	27.3	755.9
128	7	100	13.55	1.584	21.96	25.2	87	22.9	3.2	67.5	25.2	27.4	27.4	757.1
128	7.5	170	20.6	1.46	21.89	25.2	87	22.9	6.4	67.5	25.2	27.4	27.4	757.5
128	8	350	27.59	1.335	21.82	25.6	85	22.8	8	45	25.6	27.8	27.8	757.8
128	8.5	540	34.49	1.202	22.37	26.2	84	23.2	1.6	45	26.2	28.7	28.7	757.6
128	9	501	41.22	1.065	21.96	26.7	83	23.6	1.6	45	26.7	29.7	29.7	757.3
128	9.5	730	47.68	0.948	22.07	26.6	84	23.6	3.2	45	26.6	29.4	29.4	757
128	10	815	53.62	0.849	22.18	28.2	76	23.6	4.8	45	28.2	32.2	32.2	757
128	10.5	830	58.76	0.767	22.27	30.6	65	23.2	12.9	202.5	30.5	35.3	35.3	756.8
128	11	860	62.79	0.7	22.37	30.4	67	23.6	20.9	202.5	29.7	35.4	34.7	756.6
128	11.5	920	65.39	0.653	22.43	31.3	64	23.7	16.1	202.5	31.2	36.4	36.2	756.3
128	12	900	66.4	0.637	22.49	30.8	66	23.7	20.9	202.5	30.2	35.9	35.3	756.3
128	12.5	720	65.73	0.664	22.54	29.3	72	23.8	22.5	202.5	28.3	34	33	756.1
128	13	340	63.45	0.72	22.59	27.9	78	23.7	24.1	202.5	26.6	31.8	30.4	755.7
128	13.5	420	59.69	0.802	22.54	28.6	74	23.5	20.9	225	27.6	32.8	31.8	755.5

DoY	$H_r(t)$	$S_r(t)$	$S_e(t)$	$T(t)$	$S_p(t)$	$A(t)$	$H_u(t)$	$D(t)$	$W_s(t)$	$W_d(t)$	$W_c(t)$	$H_x(t)$	$T_x(t)$	$B(t)$
128	14	467	54.75	0.9	22.49	28.2	76	23.6	22.5	225	27	32.2	30.9	755.2
128	14.5	112	48.94	1.005	22.47	28.7	76	24.1	24.1	202.5	27.4	33.5	32.2	755.2
128	15	582	42.57	1.118	22.44	27.9	80	24.2	20.9	202.5	26.8	32.1	30.9	755.2
128	15.5	247	35.89	1.233	22.41	27.4	82	24.1	19.3	202.5	26.3	31.1	30	754.9
128	16	386	29.02	1.348	22.37	27.4	83	24.2	17.7	202.5	26.4	31.1	30.1	754.8
128	16.5	141	22.05	1.446	22.36	27.5	81	23.9	17.7	202.5	26.6	31.1	30.2	755
128	17	240	15	1.526	22.35	27	85	24.3	17.7	202.5	26	30.5	29.5	755.1
128	17.5	60	7.904	1.605	22.32	26.4	87	24.1	14.5	202.5	25.8	29.6	29	755.4
129	7	80	13.54	1.564	22.92	24.6	90	22.8	6.4	67.5	24.6	26.6	26.6	757.1
129	7.5	290	20.58	1.511	22.92	25.1	88	23	6.4	45	25.1	27.3	27.3	757.5
129	8	300	27.55	1.454	22.92	26.3	85	23.6	4.8	22.5	26.3	29.1	29.1	757.9
129	8.5	390	34.43	1.379	22.37	26.6	83	23.5	3.2	247.5	26.6	29.4	29.4	757.8
129	9	500	41.14	1.298	22.82	27.3	80	23.6	4.8	270	27.3	30.6	30.6	757.7
129	9.5	660	47.57	1.21	22.72	27.8	78	23.6	6.4	292.5	27.8	31.4	31.4	757.6
129	10	740	53.49	1.1	22.61	28.1	79	24.1	6.4	315	28.1	32.2	32.2	757.5
129	10.5	830	58.6	0.991	22.49	27.8	80	24	6.4	22.5	27.8	31.6	31.6	757.4
129	11	934	62.6	0.876	22.37	28.4	76	23.7	4.8	22.5	28.4	32.6	32.6	757.4
129	11.5	945	65.19	0.787	22.48	30.7	67	23.8	11.3	202.5	30.7	35.9	35.9	757
129	12	940	66.19	0.729	22.59	29.4	71	23.6	16.1	202.5	28.9	33.9	33.4	756.6
129	12.5	903	65.53	0.694	22.66	29.2	73	23.9	16.1	225	28.7	33.9	33.4	756.2
129	13	910	63.25	0.687	22.73	29.8	71	24	16.1	225	29.3	34.8	34.4	755.6
129	13.5	788	59.51	0.705	22.55	29.6	72	24	19.3	202.5	28.8	34.5	33.7	755.4
129	14	650	54.6	0.749	22.37	29.3	74	24.2	20.9	202.5	28.3	34.3	33.3	755
129	14.5	710	48.82	0.837	22.33	28.5	77	24.1	24.1	202.5	27.2	33.1	31.8	754.7
129	15	710	42.47	0.969	22.3	28.7	76	24	22.5	202.5	27.5	33.3	32.2	754.5
129	15.5	580	35.81	1.101	22.29	29.1	74	23.9	22.5	202.5	28	33.8	32.8	754.3
129	16	390	28.96	1.212	22.27	29.1	74	23.9	20.9	202.5	28.1	33.8	32.9	754.2

DoY	$H_r(t)$	$S_r(t)$	$S_e(t)$	$T(t)$	$S_p(t)$	$A(t)$	$H_u(t)$	$D(t)$	$W_s(t)$	$W_d(t)$	$W_c(t)$	$H_x(t)$	$T_x(t)$	$B(t)$
129	16.5	300	22	1.289	22.23	28.4	76	23.7	20.9	202.5	27.3	32.6	31.5	754
129	17	150	14.97	1.355	22.18	28	78	23.8	20.9	202.5	26.8	31.9	30.7	754
129	17.5	48	7.882	1.424	22.5	27.3	80	23.5	17.7	202.5	26.3	30.4	29.4	754.3
130	7	55	13.52	1.564	22.35	25.2	85	22.5	3.2	67.5	25.2	27.3	27.3	756
130	7.5	74	20.55	1.566	22.48	24.5	88	22.4	1.6	22.5	24.5	26.4	26.4	756.4
130	8	148	27.52	1.558	22.61	24.8	87	22.5	1.6	67.5	24.8	26.8	26.8	756.6
130	8.5	185	34.38	1.523	22.37	25.1	86	22.6	1.6	45	25.1	27.2	27.2	756.8
130	9	171	41.07	1.464	22.44	24.3	90	22.6	3.2	45	24.3	26.3	26.3	757
130	9.5	186	47.48	1.383	22.32	24.8	88	22.7	1.6	45	24.8	26.8	26.8	757.2
130	10	260	53.36	1.289	22.2	25.6	85	22.8	1.6	247.5	25.6	27.8	27.8	757
130	10.5	326	58.45	1.187	22.25	25.9	83	22.8	1.6	22.5	25.9	28.2	28.2	757
130	11	430	62.43	1.083	22.3	27.4	77	23.1	11.3	225	27.4	30.4	30.4	756.9
130	11.5	1130	65	0.985	22.56	27.9	77	23.5	17.7	225	26.9	31.4	30.5	756.5
130	12	972	65.99	0.893	22.82	29	73	23.7	19.3	225	28.1	33.6	32.7	756
130	12.5	600	65.33	0.811	22.54	28.6	74	23.5	22.5	225	27.4	32.8	31.7	755.8
130	13	364	63.06	0.746	22.25	29.3	68	22.8	17.7	202.5	28.6	33.1	32.4	755.4
130	13.5	564	59.34	0.707	22.18	27.8	73	22.5	16.1	202.5	27.1	30.7	29.9	755.3
130	14	190	54.45	0.697	22.11	28.9	69	22.7	16.1	202.5	28.3	32.7	32.1	755
130	14.5	293	48.7	0.714	22.14	28.8	66	21.8	14.5	180	28.4	31.7	31.3	754.9
130	15	295	42.37	0.753	22.18	28.9	65	21.6	12.9	202.5	28.7	31.8	31.6	754.8
130	15.5	600	35.73	0.815	22.23	28.9	67	22.1	14.5	202.5	28.5	32.2	31.8	754.7
130	16	420	28.89	0.893	22.27	29.7	64	22.1	12.9	180	29.6	33.2	33.1	754.6
130	16.5	121	21.95	0.993	22.09	28.4	70	22.4	12.9	202.5	28.3	31.6	31.4	754.4
130	17	90	14.94	1.113	21.92	26.9	77	22.6	12.9	202.5	26.7	29.4	29.2	754.5
130	17.5	29	7.858	1.234	21.81	26.2	80	22.5	9.7	202.5	26.2	28.4	28.4	754.7
131	7	95	13.51	1.374	21.22	25.9	83	22.8	9.7	157.5	25.9	28.2	28.2	757.7
131	7.5	100	20.53	1.412	21.04	26.3	80	22.6	12.9	180	26.1	28.6	28.4	758

DoY	$H_r(t)$	$S_r(t)$	$S_e(t)$	$T(t)$	$S_p(t)$	$A(t)$	$H_u(t)$	$D(t)$	$W_s(t)$	$W_d(t)$	$W_c(t)$	$H_x(t)$	$T_x(t)$	$B(t)$
131	8	166	27.47	1.45	20.87	26.6	79	22.7	11.3	180	26.6	29	29	758.2
131	8.5	210	34.32	1.5	22.37	27.2	77	22.8	9.7	180	27.2	29.9	29.9	758.3
131	9	275	40.99	1.55	21.29	26.5	80	22.8	9.7	157.5	26.5	28.9	28.9	758.6
131	9.5	430	47.37	1.5	21.21	26.8	80	23	4.8	67.5	26.8	29.4	29.4	758.4
131	10	476	53.24	1.45	21.13	28.7	70	22.7	12.9	202.5	28.6	32.3	32.1	758.1
131	10.5	411	58.3	1.367	21.18	28.5	73	23.2	17.7	202.5	27.7	32.3	31.6	757.9
131	11	340	62.25	1.268	21.22	28.1	75	23.2	16.1	202.5	27.3	31.6	30.8	757.9
131	11.5	409	64.8	1.158	21.26	27.9	76	23.3	16.1	202.5	27.1	31.3	30.5	757.6
131	12	470	65.79	1.054	21.29	28.6	73	23.3	17.7	202.5	27.8	32.6	31.8	757.4
131	12.5	390	65.13	0.954	21.26	28.6	73	23.2	16.1	202.5	27.9	32.4	31.8	757
131	13	555	62.87	0.85	21.22	30.3	67	23.5	17.7	202.5	29.8	35.2	34.7	756.7
131	13.5	1034	59.17	0.756	21.21	31.1	63	23.2	17.7	202.5	30.8	35.6	35.2	756.4
131	14	940	54.3	0.67	21.2	30.6	63	22.7	22.5	202.5	29.8	34.9	34.2	756.2
131	14.5	690	48.57	0.655	21.26	30.2	65	22.9	22.5	202.5	29.4	34.6	33.8	755.9
131	15	640	42.27	0.64	21.32	29.8	67	23	22.5	202.5	28.9	34.2	33.2	755.7
131	15.5	520	35.65	0.68	21.08	29.6	69	23.3	22.5	202.5	28.6	33.9	32.9	755.5
131	16	400	28.83	0.717	20.84	28.9	72	23.4	24.1	202.5	27.7	33.2	32	755.7
131	16.5	340	21.91	0.751	20.67	29	72	23.4	22.5	202.5	27.9	33.3	32.2	755.7
131	17	260	14.9	0.829	20.51	28.8	72	23.3	20.9	202.5	27.8	33	32	755.8
131	17.5	70	7.836	0.897	20.67	28.4	73	23.1	17.7	202.5	27.6	32.2	31.3	756.1
132	7	100	13.51	1.123	20.98	24.7	86	22.2	4.8	67.5	24.7	26.6	26.6	758.9
132	7.5	230	20.53	1.234	21.04	25.7	83	22.6	1.6	45	25.7	27.9	27.9	759.3
132	8	360	27.47	1.349	21.1	27.4	76	22.8	0	22.5	27.4	30.2	30.2	759.6
132	8.5	450	34.32	1.449	20.97	26.7	79	22.7	1.6	292.5	26.7	29.1	29.1	759.9
132	9	615	40.99	1.531	20.84	26.4	79	22.5	3.2	247.5	26.4	28.7	28.7	759.7
132	9.5	700	47.37	1.583	20.91	26.3	80	22.6	4.8	247.5	26.3	28.6	28.6	759.6
132	10	740	53.24	1.588	20.98	26.9	78	22.8	4.8	247.5	26.9	29.5	29.5	759.7

DoY	$H_r(t)$	$S_r(t)$	$S_e(t)$	$T(t)$	$S_p(t)$	$A(t)$	$H_u(t)$	$D(t)$	$W_s(t)$	$W_d(t)$	$W_c(t)$	$H_x(t)$	$T_x(t)$	$B(t)$
132	10.5	800	58.3	1.555	21.12	27.4	76	22.8	8	270	27.4	30.2	30.2	759.3
132	11	875	62.25	1.494	21.25	27.1	77	22.7	11.3	225	27.1	29.6	29.6	759.1
132	11.5	880	64.8	1.408	21.25	29.2	68	22.7	17.7	225	28.5	32.9	32.2	758.8
132	12	895	65.79	1.307	21.25	28.4	72	22.9	19.3	225	27.4	32	31	758.6
132	12.5	890	65.13	1.161	21.09	29.6	68	23	19.3	202.5	28.8	33.7	32.9	758.3
132	13	895	62.87	0.976	20.94	28.9	73	23.6	19.3	202.5	28.1	33.4	32.6	757.9
132	13.5	866	59.17	0.84	20.9	29.1	72	23.5	19.3	202.5	28.3	33.6	32.7	757.7
132	14	820	54.3	0.735	20.87	28.3	75	23.5	19.3	202.5	27.3	32.3	31.3	757.6
132	14.5	610	48.57	0.686	21.33	28.4	74	23.4	20.9	202.5	27.3	32.4	31.3	757.3
132	15	587	42.27	0.638	21.8	28.7	73	23.3	20.9	202.5	27.6	32.8	31.7	757.1
132	15.5	433	35.65	0.565	21.45	28.4	75	23.6	20.9	202.5	27.3	32.6	31.4	757
132	16	404	28.83	0.524	21.1	28.1	76	23.4	20.9	202.5	26.9	31.7	30.6	757
132	16.5	336	21.91	0.543	21.02	27.3	79	23.4	20.9	202.5	26	30.4	29.1	756.9
132	17	180	14.9	0.622	20.94	27.4	79	23.4	19.3	202.5	26.3	30.6	29.4	757.1
132	17.5	83	7.836	0.711	20.92	26.9	79	22.9	19.3	202.5	25.7	29.5	28.3	757.4
133	7	80	13.47	0.914	21.25	23.9	91	22.4	1.6	90	23.9	25.9	25.9	759.1
133	7.5	77	20.46	1.055	21.26	23.4	92	22	4.8	45	23.4	24.9	24.9	759.3
133	8	118	27.38	1.19	21.27	23.5	91	21.9	4.8	45	23.5	25.1	25.1	759.4
133	8.5	119	34.2	1.325	21.27	22.7	93	21.5	4.8	45	22.7	24.2	24.2	759.6
133	9	245	40.83	1.468	21.27	23.3	92	22	1.6	45	23.3	24.8	24.8	759.7
133	9.5	365	47.17	1.59	21.26	24.7	88	22.6	1.6	45	24.7	26.7	26.7	759.6
133	10	555	52.98	1.677	21.25	26.7	82	23.3	1.6	315	26.7	29.4	29.4	759.6
133	10.5	835	57.99	1.698	21.27	27.6	79	23.6	3.2	292.5	27.6	30.9	30.9	759.3
133	11	896	61.91	1.672	21.29	27.8	79	23.9	4.8	270	27.8	31.6	31.6	758.9
133	11.5	920	64.43	1.63	21.27	28.4	73	23.1	8	247.5	28.4	32.2	32.2	758.5
133	12	936	65.41	1.565	21.25	30.2	66	23.1	14.5	202.5	29.9	34.7	34.4	758.3
133	12.5	925	64.75	1.467	21.19	29.8	67	23	16.1	202.5	29.4	34.2	33.7	757.9

DoY	$H_r(t)$	$S_r(t)$	$S_e(t)$	$T(t)$	$S_p(t)$	$A(t)$	$H_u(t)$	$D(t)$	$W_s(t)$	$W_d(t)$	$W_c(t)$	$H_x(t)$	$T_x(t)$	$B(t)$
133	13	911	62.52	1.343	21.13	29.4	69	23.1	16.1	202.5	28.9	33.5	33	757.6
133	13.5	526	58.85	1.205	21.21	29.4	68	22.9	17.7	202.5	28.8	33.4	32.8	757.4
133	14	457	54.03	1.068	21.29	29.2	69	22.9	17.7	202.5	28.5	33.1	32.4	757.1
133	14.5	322	48.35	0.934	21.35	28.4	74	23.4	17.7	202.5	27.6	32.4	31.6	756.9
133	15	380	42.09	0.808	21.41	28.4	75	23.6	17.7	202.5	27.6	32.6	31.7	756.7
133	15.5	305	35.51	0.686	21.54	27.7	79	23.7	19.3	202.5	26.6	31.2	30.2	756.4
133	16	208	28.72	0.612	21.68	27.2	81	23.6	17.7	202.5	26.2	30.3	29.3	756.4
133	16.5	128	21.83	0.561	21.87	26.6	84	23.6	16.1	202.5	25.7	29.4	28.6	756.6
133	17	43	14.85	0.517	21.96	26	86	23.5	16.1	202.5	25.1	28.7	27.7	756.7
133	17.5	21	7.803	0.478	22.05	25.9	86	23.4	16.1	202.5	25	28.6	27.6	757
134	7	56	13.45	0.705	23.38	25.5	82	22.2	12.9	157.5	25.2	27.5	27.2	758.9
134	7.5	89	20.43	0.839	22.79	25.9	80	22.2	11.3	157.5	25.9	27.9	27.9	759.4
134	8	137	27.34	0.976	22.2	26.2	80	22.5	12.9	180	26	28.4	28.2	759.3
134	8.5	180	34.13	1.118	22	26.6	80	22.9	14.5	157.5	26	29.1	28.4	759.4
134	9	220	40.75	1.261	21.8	27.2	77	22.8	16.1	157.5	26.4	29.9	29.1	759.3
134	9.5	256	47.06	1.408	21.82	27.8	74	22.7	16.1	157.5	27	30.7	29.9	759.1
134	10	277	52.85	1.54	21.84	28.2	72	22.7	16.1	157.5	27.6	31.4	30.8	759
134	10.5	371	57.84	1.649	21.9	28.8	70	22.8	17.7	180	28.1	32.4	31.7	758.8
134	11	683	61.73	1.732	21.96	29.7	66	22.7	16.1	180	29.3	33.7	33.2	758.6
134	11.5	460	64.24	1.77	22.19	29.9	65	22.6	16.1	157.5	29.5	34	33.6	758.2
134	12	510	65.22	1.774	22.42	29.2	67	22.4	20.9	202.5	28.2	32.7	31.7	758
134	12.5	615	64.56	1.737	22.29	29.2	70	23.1	22.5	202.5	28.1	33.3	32.2	757.6
134	13	1020	62.34	1.654	22.15	29.8	68	23.2	22.5	202.5	28.8	34.2	33.3	757
134	13.5	680	58.7	1.54	22.18	29.6	70	23.5	22.5	202.5	28.6	34.1	33.1	757.1
134	14	500	53.9	1.395	22.2	29.4	70	23.4	22.5	202.5	28.4	33.8	32.8	756.7
134	14.5	600	48.24	1.232	22.16	29.2	69	22.9	22.5	202.5	28.1	33.1	32.1	756.2
134	15	650	42	1.068	22.11	29.7	67	22.9	24.1	202.5	28.6	33.8	32.7	755.9

DoY	$H_r(t)$	$S_r(t)$	$S_e(t)$	$T(t)$	$S_p(t)$	$A(t)$	$H_u(t)$	$D(t)$	$W_s(t)$	$W_d(t)$	$W_c(t)$	$H_x(t)$	$T_x(t)$	$B(t)$
134	15.5	360	35.44	0.905	22.05	29.2	69	22.9	22.5	202.5	28.2	33.2	32.1	756
134	16	400	28.67	0.75	21.99	29.3	69	23	22.5	202.5	28.2	33.3	32.2	756.1
134	16.5	270	21.79	0.612	22.05	29	71	23.2	22.5	202.5	27.9	33.2	32.1	756.1
134	17	160	14.82	0.499	22.11	28.9	71	23.1	19.3	180	28	32.9	32.1	756.2
134	17.5	40	7.791	0.387	22.05	28.2	72	22.6	19.3	180	27.2	31.3	30.3	756.4
135	7	77	13.43	0.461	22.35	24.4	88	22.3	8	67.5	24.4	26.3	26.3	758.1
135	7.5	156	20.4	0.574	22.58	25	85	22.3	8	67.5	25	27	27	759
135	8	198	27.29	0.688	22.82	25	86	22.5	6.4	45	25	27.1	27.1	759.2
135	8.5	250	34.07	0.823	22.37	25.1	85	22.4	6.4	67.5	25.1	27.2	27.2	758.8
135	9	590	40.67	0.978	21.92	25.5	85	22.8	9.7	45	25.5	27.7	27.7	759.2
135	9.5	675	46.96	1.144	21.95	25.6	85	22.8	11.3	45	25.6	27.8	27.8	759.1
135	10	750	52.72	1.313	21.99	25.4	87	23.1	9.7	45	25.4	27.8	27.8	759.2
135	10.5	850	57.69	1.472	21.8	27.7	76	23.1	4.8	247.5	27.7	30.9	30.9	759.4
135	11	890	61.56	1.612	21.6	28.5	72	23	12.9	225	28.3	32.1	31.9	758.9
135	11.5	890	64.06	1.718	21.22	29.4	68	22.9	20.9	225	28.5	33.3	32.4	758.9
135	12	830	65.03	1.79	20.84	28.6	72	23	24.1	202.5	27.3	32.3	31	758.3
135	12.5	860	64.38	1.815	20.78	28.3	74	23.3	25.7	202.5	26.9	32.1	30.7	758
135	13	1119	62.17	1.798	20.72	30.1	65	22.8	22.5	202.5	29.2	34.2	33.3	757.8
135	13.5	960	58.54	1.736	20.71	29.8	66	22.8	22.5	202.5	28.9	33.9	33	757.9
135	14	805	53.77	1.632	20.7	29.6	69	23.3	24.1	202.5	28.6	34.1	33	757.7
135	14.5	680	48.13	1.496	20.61	29.1	70	23	24.1	202.5	27.9	33.1	31.9	757.3
135	15	620	41.92	1.337	20.53	28.8	71	23	22.5	202.5	27.7	32.7	31.6	756.9
135	15.5	455	35.38	1.159	20.53	29.1	69	22.8	24.1	202.5	27.9	33	31.8	756.4
135	16	400	28.62	0.957	20.53	29.2	68	22.7	24.1	202.5	28	32.9	31.7	756.5
135	16.5	280	21.75	0.749	20.73	29.2	65	21.9	24.1	180	28	32.3	31.1	756.4
135	17	220	14.8	0.567	20.94	28.9	67	22.2	20.9	180	27.9	32.3	31.3	756.3
135	17.5	85	7.781	0.386	21.37	27.7	72	22.2	22.5	202.5	26.4	30.3	29	756.5

DoY	$H_r(t)$	$S_r(t)$	$S_e(t)$	$T(t)$	$S_p(t)$	$A(t)$	$H_u(t)$	$D(t)$	$W_s(t)$	$W_d(t)$	$W_c(t)$	$H_x(t)$	$T_x(t)$	$B(t)$
136	7	80	13.4	0.303	21.34	24.3	83	21.2	8	45	24.3	25.9	25.9	759
136	7.5	300	20.36	0.359	21.33	25.4	77	21.1	8	225	25.4	27	27	759.1
136	8	392	27.24	0.418	21.32	28.7	60	20.2	8	157.5	28.7	30.6	30.6	758.7
136	8.5	550	34	0.522	21.31	26.9	69	20.8	8	45	26.9	28.6	28.6	758.6
136	9	424	40.58	0.658	21.29	24.6	82	21.3	14.5	67.5	23.8	26.3	25.6	758.9
136	9.5	820	46.86	0.816	21.29	29.1	59	20.2	8	247.5	29.1	31.1	31.1	758.7
136	10	804	52.6	0.987	21.29	30.9	55	20.8	20.9	202.5	30.3	33.7	33.1	758
136	10.5	625	57.54	1.17	21.29	28.8	59	20	17.7	45	28.1	30.7	30	757.8
136	11	662	61.4	1.353	21.29	25.7	76	21.1	12.9	45	25.4	27.2	26.9	757.8
136	11.5	982	63.88	1.523	21.26	29.3	62	21.3	9.7	247.5	29.3	32.1	32.1	757.8
136	12	900	64.85	1.667	21.22	29.3	63	21.6	25.7	202.5	28.1	32.3	31.1	757.8
136	12.5	949	64.2	1.778	21.26	29.2	64	21.7	24.1	202.5	28	32.1	30.9	757.6
136	13	910	62.01	1.824	21.29	30.8	57	21.3	12.9	202.5	30.7	33.9	33.8	757.6
136	13.5	880	58.4	1.83	21.31	29.3	62	21.2	20.9	225	28.3	31.9	31	757.3
136	14	810	53.64	1.803	21.32	29.2	64	21.7	20.9	202.5	28.2	32.1	31.2	757
136	14.5	675	48.03	1.734	21.23	29.5	62	21.5	19.3	202.5	28.7	32.4	31.6	756.8
136	15	610	41.84	1.599	21.15	28.7	65	21.4	19.3	202.5	27.7	31.3	30.3	756.7
136	15.5	480	35.31	1.438	21.28	28.3	65	21.1	19.3	202.5	27.3	30.4	29.4	756.7
136	16	380	28.58	1.256	21.41	27.6	70	21.6	17.7	202.5	26.6	29.7	28.8	756.6
136	16.5	272	21.72	1.054	21.35	26.9	73	21.6	17.7	202.5	25.8	28.8	27.8	756.7
136	17	250	14.78	0.843	21.29	26.3	76	21.8	12.9	202.5	26.1	28.2	28	757
136	17.5	46	7.771	0.633	21.25	26.4	74	21.4	11.3	225	26.4	28.2	28.2	756.8

APPENDIX B

MATLAB PROGRAMS

goiguanas2011.m

```
%Front end program for parameterizing iguana models
%To run, type "goiguanas2011" at the Matlab prompt.
%author: Brianna Payne [Code for graphing from Jonathan Cowels]

global data pr residual

%load data set (see txt file names below)
%iguanas2011_SA.txt for total Sandy
%param_ig2011_SA.txt for Sandy site paramaterization/estimation data set
%val_ig2011_SA.txt for Sandy site validation data set
%iguanas2011_SB.txt for total the Rocky site
%iguanas2011_LSB.txt for the Rocky site without days 126 and 127
%iguanas2011_L6SB.txt for the Rocky site without day 126
%iguanas2011_L7SB.txt for the Rocky site without day 127
%iguanas2011_LPSB.txt for the Rocky site without day 126 1500 through 127 1230

data = load('iguanas2011_LPSB.txt');
count = data(:,3);
nmtm = data(:,1)+data(:,2)/24;

%set the initial parameter values for downhill method in the following order%

theta = log( 5.08125324535012E-06;
             0.895950884415359;
             24.0573575001896;
            1.80400496472888;
             6.76446208969124;
             2.439257184723 ]);

%call nelder routine within matlab to minimize RSS
%change iguana model in iguanamodelA2011 to try different E(t)

[output fct] = fminsearch('iguanamodel2011', theta);

%store best predictions

prediction = pr;

%print best parameters to screen

parameters = exp(output)

%print stats at best parameters
```

```
RSS = fct;

sigmasq = RSS/length(data(:,3))
kappa = length(theta)+1
AIC = length(data(:,3))*log(sigmasq) + 2*kappa
Rsq = 1 - RSS/sum((sqrt(count) - mean(sqrt(count)) ).^2)
delta = AIC - 627.4561383

%plot one week of data

day = (data(:,1)-min(data(:,1)));
for z=0:6
        %which of the 4 weeks of data should be plotted
        week = 2-1;
        arrayid = find(data(:,1) == 120+z+week*7);
                xtime = (data(arrayid,2));
                yiguan = (data(arrayid,3));
                ypred = pr(arrayid);

                %create subplots

                dayplot(z+1) = subplot(2,4,z+1);

                %plot seal numbers

                scatter(xtime,yiguan,2.5,[0 0.5 0])


                %name plot and scale axes

                axis([5 22 0 450]);
                plottitle = ['Day ',num2str(data(min(arrayid)))];
                title(plottitle);
                hold on

                %plot predictions

                plot(xtime,ypred)
end
```

iguanamodel2011.m

```
%Subroutine iguanamodel2011
%Debugged 19 Sept 2011
%Author: Brianna Payne
%Computes RSS for goiguanas2011.m
```

```
function fct = iguanamodel2011(theta)

global data pr residual

%set parameters in the following order
%ensure matches the number called for in pr and factor
%theta in goiguanas must have the same # of params

param = exp(theta);
a = param(1);
b = param(2);
g = param(3);
k = param(4);
z = param (5);
j = param (6);
%w = param (7);

%define columns of input - nondimensionalizing and scaling done in excel file

day = data(:,1);
hour = data(:,2);
count = data(:,3);
sorad = data(:,4);
sev = data(:,5);
tide = data(:,6);
seatp = data(:,7);
ambtp = data(:,8);
hm = data(:,9);
dp = data(:,10);
wdsp = data(:,11);
wdd = data(:,12);
wc = data(:,13);
hi = data(:,14);
thw = data(:,15);
bp = data(:,16);

%normalize hour

hr1 = data(:,2) - min(data(:,2));
hr2 = hr1 ./ max(hr1) + 1;
normhour = hr2;

%define environmental variable function

factor = (sev.^k.*hi.^z./(hm.^j.*tide.^w))
```

```
%compute model predictions
%Sandy site: use b.*Envelope (hard code in parameters from envelope parameterization)
% Rocky site: use (b.*sev.^g).

pr = (b.*sev.^g )./(1 + a*factor);

%Create vector of residuals

residual = sqrt(count) - sqrt(pr);

%Compute RSS, the sum of squared residuals

fct = sum(residual.^2);
```

LITERATURE CITED

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