Temporal Dynamics of Galapagos Marine Iguana (Amblyhynchus Cristatus) Haulout

Brianna Gale Payne

Anders University, brianna@andrews.edu

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ABSTRACT

TEMPORAL DYNAMICS OF GALÁPAGOS MARINE IguANA

(*Amblyrhynchus cristatus*) HAULOUT

by

Brianna Gale Payne

Co-Chairs: James L. Hayward
Shandelle M. Henson
ABSTRACT OF GRADUATE STUDENT RESEARCH

Thesis

Andrews University

College of Arts and Sciences

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

Name of researcher: Brianna Gale Payne

Name and degree of faculty co-chairs: James L. Hayward, Ph.D.; Shandelle M. Henson, Ph.D.

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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
College of Arts and Sciences

TEMPORAL DYNAMIC OF GALÁPAGOS MARINE IGUANA

(AMBLYRHYNCHUS CRISTATUS) HAULOUT

A Thesis
Presented in Partial Fulfillment
of the Requirements for the Degree
Master of Science

by
Brianna Gale Payne
2012
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APPROVAL BY THE COMMITTEE:

_________________________________________
Co-chair: James L. Hayward, Ph.D.

_________________________________________
Co-chair: Shandelle M. Henson, Ph.D.

_________________________________________
Member: Gordon J. Atkins, Ph.D.

_________________________________________
Member: H. Thomas Goodwin, Ph.D. Date approved
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 \textit{(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 (0°18’16 S, 91°39’06 W, Google Earth; 425 m²) 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 (0°18’11 S, 91°39’09 W, Google Earth; 65 m²) 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 (0°18’06” S 91°39’10”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 0° and 360° at true North and then transformed to a linear scale according to:

\[
D_{\text{linear}} = \begin{cases} 
D_{\text{circular}} & \text{if } D_{\text{circular}} \leq 180 \\
360 - D_{\text{circular}} & \text{if } D_{\text{circular}} > 180
\end{cases}
\]
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 $S$:

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

**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

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

$$Q(t) = S_e(t),$$  \hspace{1cm} (1b)

where $S_e(t)$ is the solar elevation at time $t$ and $\theta > 0$ 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:

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

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

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

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

$$0 = aE_{12}(t)(M(t) - N(t)) - bE_{21}(t)N(t) \quad (4)$$
(Hoppensteadt, 1974; Henson et al., 2006). Solving for $N(t)$ yields

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

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

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

and for the Rocky site

$$N(t) = \frac{\beta S^i}{1 + \alpha E(t)}. \quad (6b)$$

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) $\alpha, \beta, i > 0$ 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
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

\[
\ln(Q(t)) = \ln(\eta + \delta \sin(\gamma \text{day of year} + t / 24)) + \sigma \epsilon(t),
\]

or equivalently,

\[
Q(t) = \left(\eta + \delta \sin(\gamma \text{day of year} + t / 24)\right)e^{\sigma \epsilon(t)},
\]

where \(\epsilon(t)\) 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
\[
\sqrt{N(t)} = \sqrt{\frac{\beta(\eta + \delta \sin(\gamma \text{day of year} + t/24))}{1 + \alpha E(t)}} + \sigma_e(t), \quad (10)
\]

or equivalently,

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

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

\[
N(t) = \left( \sqrt{\beta S_e} + \sigma_e(t) \right)^2. \quad (11b)
\]

In (11a) and (11b), the right-hand 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

\[
RSS(\theta) = \sum_{\text{data}} (f(\text{observation}) - f(\text{prediction}))^2
\]

as a function of the vector \( \theta \) 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 \textit{fminsearch}.

I obtained parameters for sub-model (1a) by fitting it to \textit{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 $\Omega_i$ are constant parameters that can be positive, zero, or negative. Estimation of 16 or 17 parameters (14 exponents plus the coefficients $\alpha$, $\beta$, and $\iota$) 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 $\Omega_i$ 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

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

where $n$ is the number of observations, $\hat{\sigma}^2 = RSS(\hat{\theta})/n$ is the variance of the likelihood function as estimated from the minimized residuals, and $\kappa$ is the number of model parameters, including $\hat{\sigma}^2$ (Burnham and Anderson, 2002). The model with the lowest AIC value, $AIC_{\text{min}}$, is considered the best model. Models are ranked according to $\Delta_i = AIC_i - AIC_{\text{min}}$ 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

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

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 2$^\circ$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 3°C 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

\[
Q(t) = 247.679 + 125.176 \sin(0.448089(\text{day of year } + t / 24)) \tag{12}
\]
with $R^2 = 0.918$. The period of this sine wave $(2\pi / 0.448089)$ 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

$$E(t) = \frac{S_e H_x}{H_u T^\rho},$$ (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

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

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

$$E(t) = \frac{S_e A}{H_u T^\rho},$$ (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

$$N(t) = \frac{\beta (247.7 + 125.2 \sin(0.4481 \text{day of year} + t / 24)))}{1 + \alpha \left( \frac{S_e H_x}{H_u T^\rho} \right)}$$ (16)
where $\beta = 0.89595$, $\alpha = 5.0812E-06$, $\varsigma = 24.057$, $\phi = 1.8040$, $\psi = 6.7644$, $\rho = 2.4393$, 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 $\Delta_i < 10$ (Table 3). The best model for the Rocky site ($\Delta_i = 0$, $R^2 = 0.567$) has environmental function

$$E(t) = \frac{S^\varsigma T_x^{\alpha}}{H_r^\varsigma T_x^\rho}, \quad (17)$$

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

$$E(t) = \frac{S^\varsigma H_x^{\phi}}{H_r^\varsigma T_x^\rho}, \quad (18)$$

and the third model ($\Delta_i = 9.550$, $R^2 = 0.5556$) has environmental function
\[ E(t) = \frac{S^e W^e}{H^e T^e}, \quad (19) \]

where \( W^e \) 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

\[ N(t) = \frac{\beta S^e}{1 + \alpha \left( \frac{S^e r^\omega}{H^e T^\rho} \right)} \quad (20) \]

where \( \beta = 198.41, \alpha = 0.94372, \varsigma = 17.857, \omega = 5.6945, \zeta = 4.7029, \rho = 3.2322 \), 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

$$N(t) = \beta (247.7 + 125.2 \sin(0.4481 (\text{day of year} + t / 24))) \frac{1}{1 + \alpha \left(\frac{\tau}{T^2}\right)^{\beta}},$$

where $\beta = 0.90210$, $\alpha = 4.6447E-07$, $\tau = 25.683$, and $\rho = 2.3556$, 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

$$N(t) = \frac{\beta S_e^\tau}{1 + \alpha \left(\frac{S_e^\tau}{H^2 T^0}\right)},$$

where $\beta = 197.07$, $\tau = 0.96393$, $\alpha = 1.4863E-05$, $\zeta = 21.849$, $\bar{\zeta} = 3.5498$, and $\rho = 3.0910$, 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 10° increase in solar elevation), but efflux also increases at an even greater rate (89% for a 10° 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 10° 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 10° 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 $\Delta t < 10$ 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 35°C, 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 40°C (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 $I_0$ 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 $I_0(1+\alpha E(t))$.

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.

<table>
<thead>
<tr>
<th>Environmental factor</th>
<th>Variable</th>
</tr>
</thead>
<tbody>
<tr>
<td>Solar radiation</td>
<td>$S_r(t)$</td>
</tr>
<tr>
<td>Solar elevation</td>
<td>$S_e(t)$</td>
</tr>
<tr>
<td>Tide Height</td>
<td>$T(t)$</td>
</tr>
<tr>
<td>Seawater temperature</td>
<td>$S_p(t)$</td>
</tr>
<tr>
<td>Ambient temperature</td>
<td>$A(t)$</td>
</tr>
<tr>
<td>Relative humidity</td>
<td>$H_u(t)$</td>
</tr>
<tr>
<td>Dew point</td>
<td>$D(t)$</td>
</tr>
<tr>
<td>Wind speed</td>
<td>$W_f(t)$</td>
</tr>
<tr>
<td>Wind direction</td>
<td>$W_d(t)$</td>
</tr>
<tr>
<td>Wind chill</td>
<td>$W_c(t)$</td>
</tr>
<tr>
<td>Heat index</td>
<td>$H_x(t)$</td>
</tr>
<tr>
<td>THW index</td>
<td>$T_x(t)$</td>
</tr>
<tr>
<td>Barometric pressure</td>
<td>$B(t)$</td>
</tr>
<tr>
<td>Hour of day</td>
<td>$H_r(t)$</td>
</tr>
</tbody>
</table>

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.

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

<table>
<thead>
<tr>
<th>Sandy site</th>
<th>Rocky site</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S_e H^p / H_u T^p$</td>
<td>$S_e T^o / H_u T^p$</td>
</tr>
<tr>
<td>5.89</td>
<td>5.41</td>
</tr>
<tr>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>0.7713*</td>
<td>0.5671*</td>
</tr>
<tr>
<td>$S_e T^o / H_u T^p$</td>
<td>$S_e H^p / H_u T^p$</td>
</tr>
<tr>
<td>5.90</td>
<td>5.42</td>
</tr>
<tr>
<td>0.3478</td>
<td>0.4943</td>
</tr>
<tr>
<td>0.7711</td>
<td>0.5665</td>
</tr>
<tr>
<td>$S_e A^c / H_u T^p$</td>
<td>$S_e W^o / H_u T^p$</td>
</tr>
<tr>
<td>5.90</td>
<td>5.56</td>
</tr>
<tr>
<td>0.7241</td>
<td>9.550</td>
</tr>
<tr>
<td>0.7709</td>
<td>0.5556</td>
</tr>
<tr>
<td>$S_e W^o / H_u T^p$</td>
<td>$S_e A^c / H_u T^p$</td>
</tr>
<tr>
<td>5.92</td>
<td>5.64</td>
</tr>
<tr>
<td>1.468</td>
<td>14.46</td>
</tr>
<tr>
<td>0.7705</td>
<td>0.5495</td>
</tr>
<tr>
<td>$S_e H^c / H_u T^p$</td>
<td>$S_e S^o / H_u T^p$</td>
</tr>
<tr>
<td>5.95</td>
<td>5.71</td>
</tr>
<tr>
<td>1.670</td>
<td>18.95</td>
</tr>
<tr>
<td>0.7691</td>
<td>0.5438</td>
</tr>
<tr>
<td>$S_e W^c / H_u T^p$</td>
<td></td>
</tr>
<tr>
<td>5.95</td>
<td></td>
</tr>
<tr>
<td>3.667</td>
<td></td>
</tr>
<tr>
<td>0.7691</td>
<td></td>
</tr>
</tbody>
</table>
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. $\Delta_i$ values are in reference to best models for each site as given in Table 3.

<table>
<thead>
<tr>
<th></th>
<th>Sandy site</th>
<th>Rocky site</th>
</tr>
</thead>
<tbody>
<tr>
<td>$E(t)$</td>
<td>$\sigma^2$</td>
<td>$\Delta_i$</td>
</tr>
<tr>
<td>$\frac{S^i}{T^p}$</td>
<td>7.10</td>
<td>68.0</td>
</tr>
<tr>
<td>$S^i$</td>
<td>7.55</td>
<td>89.9</td>
</tr>
<tr>
<td></td>
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<td></td>
<td></td>
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</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Variables</th>
<th>C (↑)</th>
<th>Sandy site</th>
<th></th>
<th>Rocky site</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Influx/ Efflux</td>
<td></td>
<td>Haulout</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$\beta$</td>
<td>$P$</td>
<td>$\beta$</td>
<td>$P$</td>
</tr>
<tr>
<td>$S_r (t)$</td>
<td>200 w/m$^2$</td>
<td>-</td>
<td>-</td>
<td>0.001*</td>
<td>27 (↑)</td>
</tr>
<tr>
<td>$S_e (t)$</td>
<td>10.0°</td>
<td>0.056*</td>
<td>75 (↑)</td>
<td>0.064*</td>
<td>89 (↑)</td>
</tr>
<tr>
<td>$T (t)$</td>
<td>0.5 m</td>
<td>-0.320</td>
<td>15 (↓)</td>
<td>-1.010*</td>
<td>40 (↓)</td>
</tr>
<tr>
<td>$S_p (t)$</td>
<td>0.5° C</td>
<td>-0.633*</td>
<td>27 (↓)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>$A (t)$</td>
<td>1.0° C</td>
<td>-1.437</td>
<td>76 (↓)</td>
<td>-1.408</td>
<td>76 (↓)</td>
</tr>
<tr>
<td>$H_u (t)$</td>
<td>5.0 %</td>
<td>-0.377*</td>
<td>85 (↓)</td>
<td>-0.323</td>
<td>80 (↓)</td>
</tr>
<tr>
<td>$W_d (t)$</td>
<td>22.5°</td>
<td>0.006</td>
<td>15 (↑)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>$W_s (t)$</td>
<td>5.0 m/s</td>
<td>0.046*</td>
<td>26 (↑)</td>
<td>-0.0588*</td>
<td>25 (↓)</td>
</tr>
<tr>
<td>$D (t)$</td>
<td>0.1° C</td>
<td>1.805*</td>
<td>20 (↑)</td>
<td>1.337</td>
<td>14 (↓)</td>
</tr>
<tr>
<td>$B (t)$</td>
<td>1.0 mm Hg</td>
<td>-0.740*</td>
<td>52 (↓)</td>
<td>0.244*</td>
<td>28 (↑)</td>
</tr>
</tbody>
</table>

Coefficient of Dispersion: Sandy site 3.016, Rocky site 4.218, - 5.618

* $p < 0.01$
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.
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 $>\frac{2}{3}$ 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.

<table>
<thead>
<tr>
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<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>123</td>
<td>1000</td>
<td>-11</td>
<td>0</td>
<td>129</td>
<td>1140</td>
<td>-47</td>
<td>10</td>
<td>133</td>
<td>1240</td>
<td>-12</td>
<td>1</td>
</tr>
<tr>
<td>123</td>
<td>1230</td>
<td>-5</td>
<td>6</td>
<td>129</td>
<td>1200</td>
<td>-50</td>
<td>7</td>
<td>133</td>
<td>1250</td>
<td>-3</td>
<td>10</td>
</tr>
<tr>
<td>124</td>
<td>1030</td>
<td>-3</td>
<td>45</td>
<td>129</td>
<td>1200</td>
<td>-50</td>
<td>7</td>
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<td>124</td>
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<td>7</td>
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<td>1040</td>
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<td>25</td>
</tr>
<tr>
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### Table A-2. Entire Data Sets for Haulout: Sandy and Rocky Sites.

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<td>17.7</td>
<td>202.5</td>
<td>26.6</td>
<td>29.7</td>
<td>28.8</td>
<td>756.6</td>
</tr>
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<td>25.8</td>
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<td>225</td>
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<td>28.2</td>
<td>28.2</td>
<td>756.8</td>
</tr>
</tbody>
</table>
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)
%iguana2011_SA.txt for total Sandy
%param_ig2011_SA.txt for Sandy site parameterization/estimation data set
%val_ig2011_SA.txt for Sandy site validation data set
%iguana2011_SB.txt for total the Rocky site
%iguana2011_LSB.txt for the Rocky site without days 126 and 127
%iguana2011_L6SB.txt for the Rocky site without day 126
%iguana2011_L7SB.txt for the Rocky site without day 127
%iguana2011_LPSB.txt for the Rocky site without day 126 1500 through 127 1230

data = load('iguana2011_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('iguana2011', theta);

%store best predictions
prediction = pr;

%print best parameters to screen
parameters = exp(output)

%print stats at best parameters
RSS = fct;

\[
sigmasq = \frac{RSS}{\text{length}(\text{data}(:,3))}
\]

\[
kappa = \text{length}(\theta) + 1
\]

\[
AIC = \text{length}(\text{data}(:,3)) \cdot \log(\text{sigmasq}) + 2 \cdot \kappa
\]

\[
Rsq = 1 - \frac{RSS}{\sum((\sqrt{\text{count}} - \text{mean}(\sqrt{\text{count}}))^2)}
\]

\[
delta = AIC - 627.4561383
\]

%plot one week of data

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

%create subplots 
\[
\text{dayplot}(z+1) = \text{subplot}(2,4,z+1);
\]

%plot seal numbers 
\[
\text{scatter}(\text{xtime},\text{yiguan},2.5,\text{[0 0.5 0]})
\]

%name plot and scale axes 
\[
\text{axis}([5 22 0 450]); 
\text{plottitle} = \text{['Day ',num2str(\text{data}(\text{min}(\text{arrayid})))]}; 
\text{title}(\text{plottitle}); 
\text{hold on}
\]

%plot predictions 
\[
\text{plot}(\text{xtime},\text{ypred})
\]
end

\text{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);
hi = data(:,14);
hi = data(:,14);
hi = data(:,14);
hi = data(:,14);

%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);
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