

Chapter 1

An Agent-Based Model of the Spatial Distribution and Density of the Santa Cruz Island Fox

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ABSTRACT

During the 1990s, the endemic Santa Cruz island (SCI) fox (*Urocyon littoralis santacruzae*) population experienced heavy predation from invasive golden eagles (*Aquila chrysaetos*) and nearly went extinct. The Island Fox Recovery Program instituted in 2002 has since reestablished the population to normal levels. We have constructed an agent-based model (ABM), which simulates the population dynamics of the SCI foxes in both the absence and presence of golden eagle predation. Geographic information system (GIS) data are integrated into the model to replicate the distribution of multiple vegetation types on the island, and the location of golden eagles' nests and hunting territories. Using the model, we determine how both island vegetation and predation by golden eagles impacted the spatial density and distribution of the foxes across SCI. Model analysis shows the 10 golden eagles known to reside on the island during the 1990s and 2000s were sufficient to have caused this rapid population decline even without the presence of other factors such as disease or competition. Additionally, model analysis shows that while removal of the golden eagles was necessary for the survival of the SCI fox population, the remaining population of 75–100 foxes had a 90% survival probability without aid. The model we present provides a powerful tool for understanding the spatial and temporal dynamics of the SCI fox population, can be used and adapted to facilitate the further management of the population, and provides a working example in integrating GIS data with ABMs.

Keywords: Predator–prey dynamics, Santa Cruz island fox, Golden eagle, Spatial dynamics, Agent-based model, Numerical simulation, Geographic information system data

1 INTRODUCTION

Many species coexist within the varied vegetation of the California Channel Islands, yet few are endemic (Collins and Latta, 2006). One such species is a small canid known as the island fox (*Urocyon littoralis*). This derivative of the mainland gray fox likely traveled to Santa Cruz island (SCI) by land bridges and adapted a dwarfed stature over thousands of years (Collins, 1991). During mating season (late January to March), mated pairs form between individuals within close geographic proximity (Moore and Collins, 1995). Island foxes are monogamous with mated pairs maintained until one member of the pair dies (Coonan, 2003). Once a mated pair is established, they attempt to find a suitable territory. This territory must be both unoccupied (by another fox mated pair) and habitable (within grassland or mixed vegetation, see Fig. 6). Island fox territory size depends on the vegetation in which the mated pair settles. If the potential territory is mainly grassland, then the territory size will be $\sim 0.87 \text{ km}^2$, but if the potential territory contains more mixed vegetation then the territory size will be $\sim 0.36 \text{ km}^2$ (Coonan, 2003; Roemer et al., 2001). Mated island foxes will attempt to reproduce during breeding season (Moore and Collins, 1995). Gestation lasts 50–53 days, and typical litter sizes are between one and three pups (Moore and Collins, 1995). Pups remain in their natal territory for the first year of their lives, after which they search for their own mates and territories (Coonan, 2003).

Invasive to the island were a population of golden eagles (*Aquila chrysaetos*) (Collins and Latta, 2009). Initially bald eagles (*Haliaeetus leucocephalus*) were the apex predator of SCI, mainly eating fish rather than preying on terrestrial species (Clark, 2009). However, by the 1950s there were no more breeding bald eagles on the island due to DDT in the water causing eagles egg shells to thin; all remaining bald eagles migrated off the island in the 1960s (Clark, 2009). The departure of bald eagles from SCI opened a niche for golden eagles to migrate from the mainland and establish territory on the island (Collins and Latta, 2006). Golden eagles are large raptors with a wingspan of up to two meters and weighing between 3.6 and 5.7 kg (Todd, 2000). Due to their large size, golden eagles require 200–300 g of food daily (Todd, 2000). They are opportunistic specialists in their feeding habits, often exhibiting a consistent preference for a specific prey until that prey diminishes, at which point they will feed on more diverse prey (Collins and Latta, 2006; Todd, 2000). Mated pairs of golden eagles hunt within territories they establish around their nests (known as eyries) with territories areas ranging from 25 to 145 km^2 where the territories of mated pairs can marginally overlap (see Fig. 1) (Todd, 2000). However, during eagle breeding season (March to August), eagles hunt within a significantly reduced area (1.6–40 km^2) centered around their eyries, and these reduced hunting regions do not overlap with other mated eagle pairs (Todd, 2000). We will refer to these smaller regions as *breeding territories* and the larger regions as *hunting territories* (Todd, 2000). Golden eagle

mated pairs maintain multiple eyries (Collins and Latta, 2006; Todd, 2000). Each breeding season, eagles choose one of their eyries for mating, at which point it becomes the center of the mated pair’s breeding territory (see Fig. 7) (Collins and Latta, 2006; Todd, 2000). Over several years, a mated pair will cycle through each of its eyries (Todd, 2000). Based on observation and nest excavation, five mated pairs once occupied SCI, with first sightings occurring around 1995 (Collins and Latta, 2006). Fig. 1 shows the nest locations and hunting territories of each of the five mated pairs on SCI using data from Collins and Latta (2006) and Latta (2004).

In the early 1990s, conservationists observed a rapid population decline of island fox populations. In 1994, the island fox population on SCI was estimated to be 1465. By 2004, that number had declined to between 75 and 100 foxes (see Fig. 2) (Coonan, 2003). The main reason for this decline was

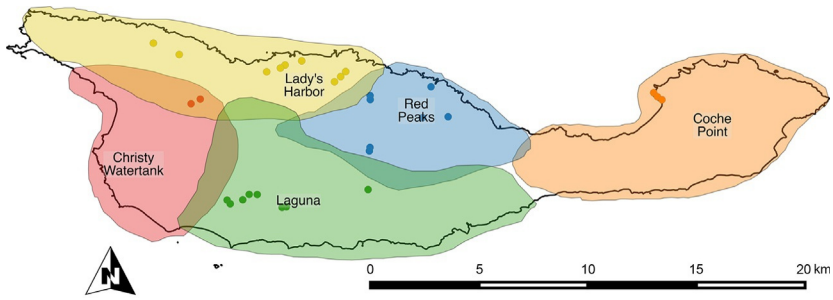


FIG. 1 Map of eagle nest locations and hunting territories on Santa Cruz island using data from Collins and Latta (2006) and Latta (2004). Each shaded region represents eagle mated pair hunting territory. Each corresponding colored dot represents a mated pair nest location. During the annual breeding season, paired eagles will choose a nest within their hunting territory at random and create a breeding territory encompassing this nest.

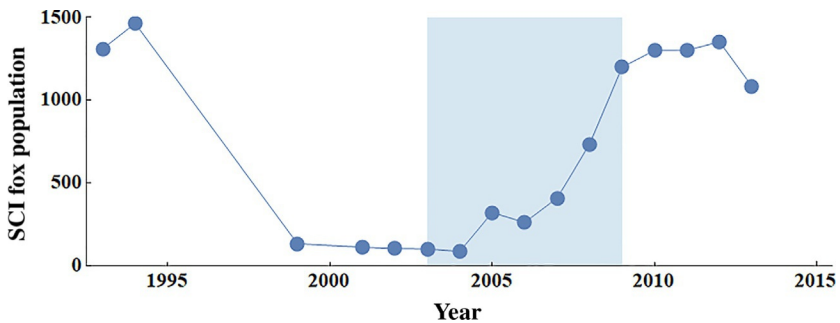


FIG. 2 The SCI island fox population size in the 1990s–2000s. The data points are taken from Island Fox Recovery Annual Reports for 1999–2013 and other observational studies (Bakker et al., 2003; Coonan, 2003, 2008, 2009, 2010, 2011, 2012, 2013, 2014; Coonan and Dennis, 2006, 2007; Coonan and Rutz, 2001; Coonan et al., 2010; Roemer et al., 2001, 2002; Schwemm, 2008). The blue shaded area represents times when recovery efforts took place.

predation by golden eagles, though disease and competition may have also had an effect (Coonan, 2003; Scott et al., 2014). In a previous study, we developed an agent-based model (ABM) that demonstrated the existence of an emergent Allee effect within the SCI fox population (Scott et al., 2014). Furthermore, we determined that the presence of a detrimental recessive allele that reduces the probability of successful reproduction could exacerbate negative per capita growth rates at low population sizes (Scott et al., 2014).

The model presented here focuses on the population dynamics of the island fox under golden eagle predation. Classical mathematical models of predator–prey interactions use the Lotka–Volterra method or other systems of equations (i.e., Kermack–McKendrick or Jacob–Monod models) (Hoppensteadt, 2006). These models are mainly useful for relatively large populations of both predators and prey, which is not the condition for SCI (Hoppensteadt, 2006). Because we assume the population sizes of both the predator and the prey are small, the results of stochastic decisions and individual interactions heavily impact population dynamics and viability. Therefore, agent-based models (ABMs) are more appropriate.

ABMs are a class of mathematical and computational models in which individuals (or agents) are unique and autonomous entities that can locally interact with other individuals, as well as with their environment (Railsback and Grimm, 2005, 2011; Scott et al., 2014). This class of models is best used for scientific questions in which interactions between agents are complex, when spatial considerations are crucial, when heterogeneous and complex topological interactions between agents are present, and when the agents included exhibit complex behavior (Bonabeau, 2002; Heppenstall et al., 2012). While equation-based models can be used in these cases, their assumptions often mask the inherent fluctuations and heterogeneity of the systems in question (Bonabeau, 2002). For example, aggregate flow equations may be used when looking at movement of collectives, but the equations usually assume homogeneous mixing (Bonabeau, 2002). In reality, the interaction network of the individuals within the collective can lead deviations from expected aggregate behavior (Bonabeau, 2002). The inclusion of stochastic processes and heterogeneity allows for emergent behaviors to be observed (Railsback and Grimm, 2011). An important feature of ABMs is the ability to inform environmental characteristics. Not only can these characteristics be defined directly by the user, but many ABM softwares also have the ability to integrate GIS data, enhancing the heterogeneous spatial realism of the model (Heppenstall et al., 2012). ABMs are applicable at a wide range of scales and in a wide range of fields, from human behavior to cellular dynamics and ecological systems (Bonabeau, 2002; Cannata et al., 2013; Conner et al., 2008; Gaff, 2011). The ABM we have developed incorporates both fox and eagle behavior and interactions, along with spatial data specific to SCI, to create a realistic, spatially explicit, multiagent-based model.

The remainder of this chapter presents a detailed description of our fox–eagle ABM and the results of several different model analyses. Specifically,

[Section 2](#) describes the types of GIS data used and how the GIS data were incorporated into the model. Within the section we provide some discussion about considerations that must be made specifically when importing and exporting GIS data in the ABM software NetLogo ([Wilensky, 1999](#)). [Section 3](#) describes the model in detail using the Overview, Design Concepts, and Details (ODD) Protocol proposed by [Grimm et al. \(2010\)](#), [Railsback and Grimm \(2005\)](#), and [Railsback and Grimm \(2011\)](#). In [Section 4](#), the results from simulations of the model under various conditions are presented. Lastly, [Section 5](#) discusses what can be concluded from the simulations and discusses the implications of the model.

2 INCORPORATING GIS DATA INTO AN ABM

Geographic Information Systems (GIS) are used to manipulate, analyze, and present geographic and spatial data. Numerous platforms with varying functionalities and price-ranges exist to perform these geographic analyses. ArcMap and QGIS are two commonly used software platforms that can be used to edit and analyze geospatial data ([ESRI, 2011](#); [QGIS Development Team, 2009](#)). QGIS software was used for all geospatial analyses in this project. The purpose of these analyses using GIS techniques was to create and manipulate data that can inform the agent-based model presented in [Section 3](#) and to analyze geospatial data that was generated from model simulations (see [Section 4](#)).

2.1 GIS Data Types

Two types of data are often used in GIS analyses: raster and vector data. Raster data is defined by matrices of pixels, such as satellite imagery or hand-drawn maps, while vector data is defined by points, lines, and polygons. In order to be imported into the ABM software NetLogo, all data must to be in vector form ([Wilensky, 1999](#)). Additionally, each vector item (point, line, or polygon) can have attributes associated with it in addition to its geographic coordinates. For example, the fox location data not only includes the latitude and longitudes of the foxes, but it also includes the year and week at which the point is recorded, allowing us to look at the changes in spatial distribution over time (see density maps generated from simulations shown in [Section 4](#)).

For the fox–eagle ABM we import data on vegetation type, which is composed of polygons (see [Fig. 3](#) for a zoomed in region of the vegetation map showing the polygons more clearly) and data on the locations of golden eagle eyries and their hunting territories (see [Fig. 1](#)). Note the locations of the eyries are stored as points while the hunting territories are stored as polygons.

The vegetation data were taken from a spatial database created by [Cohen et al. \(2009\)](#). Aerial photos were broken down by vegetation type, fennel category, and a cover rating ([Cohen et al., 2009](#)). To determine vegetation type,

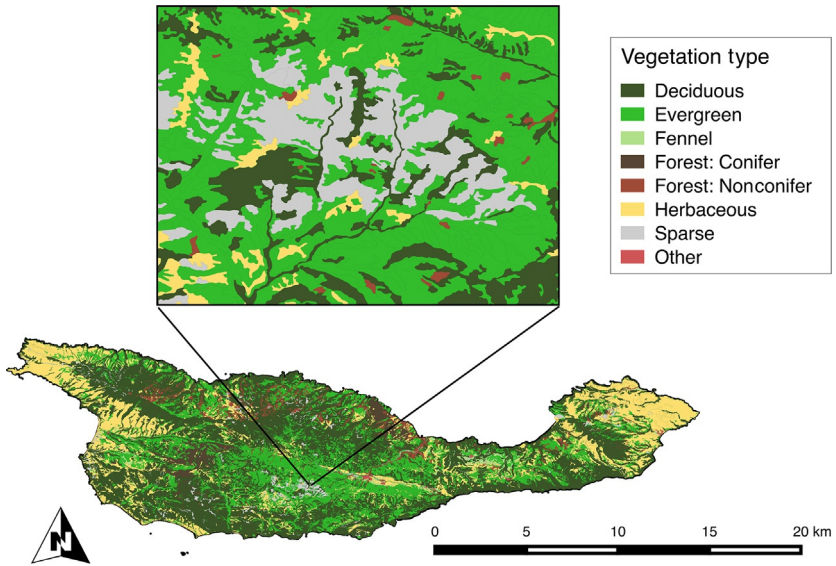


FIG. 3 The vegetation composition of Santa Cruz island classified by vegetation type. The zoomed in portion more clearly shows the polygons defining the area of each category. Data used to create this map was from [Cohen et al. \(2009\)](#).

the photos were broken down into eight vegetation groups: deciduous forest, evergreen forest, conifer woodlands, nonconifer woodlands, fennel, herbaceous, sparse, and an “other” category that accounts for nonvegetative areas (see [Fig. 3](#)) ([Cohen et al., 2009](#)). For our purposes, we were only concerned with the eight vegetation groups because fox territoriality depends on vegetation type ([Cohen et al., 2009](#)). We therefore divided these eight vegetation groups into grassland, mixed, or uninhabitable vegetation types. The forest and woodland groups were considered to be “mixed” vegetation, while the fennel and herbaceous groups were considered to be “grasslands.” The sparse and other groups were considered to be “uninhabitable” for foxes (see [Table 1](#) and [Fig. 6](#)) ([Cohen et al., 2009](#)).

The eagle hunting territories were taken from Latta’s report on golden eagle translocation ([Latta, 2004](#)). The map of territory boundaries was overlaid with the map of SCI and a polygon layer was created using the Freehand Editing plugin ([QGIS Development Team, 2009](#)). Eagle breeding territories were created by creating circles with area 25 km^2 (radius 2.8217) around each nest site and creating a new polygon layer of each territory (see [Figs. 1](#) and [7](#)) ([Collins and Latta, 2006](#); [Todd, 2000](#)).

After the model simulations are run, we create and load the location data into QGIS and run the Heatmap plugin. The produced raster images are then rectified onto the map of the island and used to show the spatial density of foxes both with and without golden eagle predation (see density maps generated from simulations shown in [Section 4](#)) ([QGIS Development Team, 2009](#)).

2.2 Projections and Coordinate Systems for GIS Data

Projections and Coordinate Systems vastly affect the way data are displayed and measured in GIS. Geographic coordinate systems are systems of latitude and longitude, which use the equator as zero degrees and form parallel lines of latitude North and South and longitude East and West. Projections are used to “project” the three-dimensional surface of the Earth onto a two-dimensional plane by converting geographic coordinates into an (X, Y) coordinate system, where X is longitude and Y is latitude, or by projecting the surface of a sphere onto a cone or cylinder, and then cutting and unrolling the cone or cylinder into a flat surface. Distortions will always exist when projecting the surface of a sphere onto a plane, so an appropriate projection must be chosen for every map to minimize distortion in the area of interest.

In a *conic projection*, the surface of the Earth (approximated as a sphere) is projected on to the surface of a cone. The projection is created by intersecting a cone with the globe. In a *tangent conic projection* the cone creates only one curve of intersection (see Fig. 4A). The dimensions of the cone are chosen such that the curve of intersection forms a circle that represents a single latitude (or an ellipse that crosses multiple latitudes if using an oblique conic projection). Fig. 4A shows the former case where the curve of intersection occurs at a single latitude, 30 degrees above the equator (i.e., 30 degrees N) in this case (shown in green). When the surface of the Earth is then projected onto the cone, there is no distance distortion at the latitude of intersection. The further away points are from the latitude of intersection, the greater the distortion of distance between them. In a *secant conic projection*, the cone intersects the globe at two latitudes called *standard parallels* (see Fig. 4B), thus creating two latitudes where no distance distortion occurs. Once the surface of the globe is projected onto the surface of the cone, the cone is cut and unfurled to create a flat surface containing the projected map (see Fig. 4C).

There are a variety of transformations which describe how the points on the globe are mapped to the surface of the cone. Two commonly used projections are *Albers Conic Equal-Area Projection* and *Lambert Conformal Conic*. Both methods use secant conic projections. The Albers projection was formulated to make all areas on the projected map have proportionally the same area as on Earth (the globe) (ESRI, 2011); see Weisstein (n.a.-a) for transformation equations. The Lambert projection, on the other hand, was formulated to maintain angles between latitude and longitude lines which minimizes shape distortion over small areas (ESRI, 2011); see Weisstein (n.a.-b) for transformation equations. The projected map in Fig. 4C uses the Albers conic equal-area projection with standard parallels of 20 degrees N (red) and 50 degrees N (blue).

For our purposes, a projection was needed that could minimize the distortion of Santa Cruz island off the coast of California. However, we also had to consider the compatibility of the agent-based modeling software, NetLogo, to handle projections. NetLogo does not support *all* projected coordinate systems. A full list of the supported projected coordinate reference systems

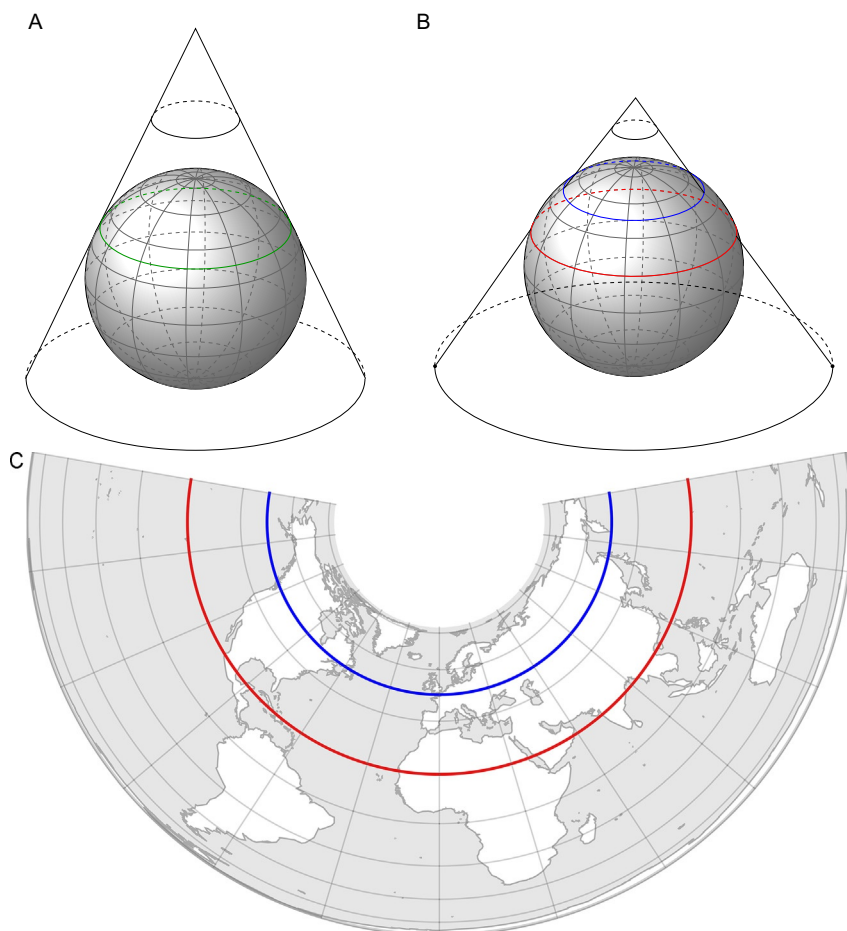


FIG. 4 A conic projection of the earth projects the surface of the globe (approximated as a sphere) onto the surface of a cone. Along the curve(s) where the cone and sphere intersect, there is no distortion in measures of distance in the projection. In the examples shown here, the tangent curve of intersection occurs at latitude 30 degrees (*green*) above the equator in (A), and the secant curves of intersection occur at the standard parallels of 20 degrees (*red*) and 50 degrees (*blue*) above the equator in (B) and (C). The projected surface in (C) uses an Albers (conic) projection.

(CRS) can be found the NetLogo documentation ([Wilensky, 1999](#)). The conic projections supported by NetLogo include

- Albers conic equal area
- Lambert conformal conic 2SP
- Polyconic
- Equidistant conic

We used the Albers conic equal-area projection with CRS NAD83 for North America (EPSG:4269) for all maps other than the vegetation map. For this map, we used the Albers conic equal-area projection with CRS NAD83/California Albers (EPSG:3310). These projections were chosen due to their abilities to minimize data distortion while remaining compatible with NetLogo software.

3 MODEL DESCRIPTION

The description of the agent-based model presented here uses the Overview, Design Concepts, and Details (ODD) Protocol as described in [Grimm et al. \(2010\)](#), [Railsback and Grimm \(2005\)](#), and [Railsback and Grimm \(2011\)](#).

3.1 Overview

3.1.1 Purpose

The purpose of this model is to simulate the population dynamics of the SCI fox and to determine the resulting effects on the island fox spatial distribution and population viability under golden eagle predation. This allows us to observe the impact of golden eagle predation on the population of island foxes. The model incorporates golden eagle and island fox behaviors to realistically replicate individual decisions and species interactions. Additionally, the model makes use of GIS data of SCI vegetation and golden eagle nest sites and territory ranges. We therefore realistically constrain the establishment of island fox territories and the hunting behaviors of the golden eagles based on this data. We use the model to (i) simulate the population decline seen on the island in the early 1990s, (ii) determine population size-dependent population viability of the island foxes in the presence and absence of golden eagle predation, and (iii) observe spatio-temporal distribution of island foxes under golden eagle predation.

3.1.2 Entities, State Variables, and Scales

The agents in this model are male foxes, female foxes, eagles, and alternative food sources (AFS) for the eagles. Both male and female foxes have state variables for their age, number of offspring, whether they have established a territory, the area (in km^2) of their territory (set to 0 if they have not established a territory), the number of attempts at forming a territory, and their mass (in kg). Each female fox additionally has a state variable for her gestation week (set to 0 if not currently gestating offspring). Each eagle has state variables for the mass of prey (in kg/wk) consumed, the number of hunting attempts during the current time step, an id number for their hunting territory and breeding territory, probability of consuming foxes over AFS, the number of foxes consumed per week, and a Boolean variable as to whether they have

or have not consumed at least one fox within a given week. Finally, each AFS has a variable determining its mass (in kg).

Each patch within the model represents a physical location with area 0.0049 km^2 ($0.07 \text{ km} \times 0.07 \text{ km}$), which is determined through integration of GIS data into the model (Cohen et al., 2009). Each patch has state variables for the patch vegetation type and vegetation group, which defines the majority of vegetation type present in that patch, based on GIS data (Collins and Latta, 2006). Patches also have an owner variable that indicates the fox that has made a territory there, and a variable indicating whether the patch is land or water. Lastly, each patch has Boolean variables determining whether the patch is part of a specific eagle hunting or breeding territory. GIS data for island vegetation type and eagle hunting and breeding territories are imported in the initialization procedure (see Section 3.3.1 for details; Cohen et al., 2009).

The model's global parameters include GIS datasets for the island, the eagle breeding territories, the eagle hunting territories, and the island vegetation. There are also variables for the number of patches on the island and several temporary variables that allow GIS data to be integrated into the model based on the associated attribute tables. Global parameters for foxes include successful reproduction rate, reproductive age, territory search radius, size, a counter for the number of foxes, a current mate variable, and a count of the overall fox offspring produced. There are also global variables pertaining to AFS, which include proportions of the total island biomass each type of AFS composes, the percent of each AFS type that composes an eagle's weekly diet, the number of each type of AFS created, the size of the AFS agents, and the total biomass of AFS present on the island. The model includes observational global variables for the number of foxes present at week 25 each year (for yearly population counts), the per capita growth rate of the fox population from the initial population size, and the yearly per capita growth rate of the fox population. There are also week and year counters.

Lastly, each time step (tick) represents 1 week and the simulation runs until there are no remaining foxes or 200 years (10,400 weeks) have passed.

3.1.3 Process Overview

The model is initialized with a user-defined number of male and female foxes on the island. The foxes are distributed across the island randomly. Those of reproductive age attempt to form mated pairs and successful mated pairs are placed into territories. Ten eagles (consistent with the number of verified nesting pairs on the island) are initialized and pairs are placed in each hunting territory (see Fig. 1) (Collins and Latta, 2006; Latta, 2004).

At each tick, foxes attempt to mate with the opposite sex (see DISPERSE and MAKE-FOX-TERRITORY submodels). If a successful mated pair is formed, the female fox will attempt to produce offspring based on the successful reproduction rate (see BREED-FOXES submodel). If the female is successful, she will

produce offspring (see BIRTH submodel). Impregnated female foxes increase their gestation by one and the age of all foxes (counted in weeks) is incremented. AFS are distributed around the island as alternative food sources for the eagles (see DISTRIBUTE-FOOD submodel). The eagles then set their energy to zero and begin to feed until they reach their minimum weekly energy requirements (see FORAGE submodel). The week counter is incremented and, once 52 weeks have passed, the year counter is incremented. The foxes die naturally based on a stochastic decision (see DEATH submodel). Lastly, the total number of foxes is calculated at the end of each time step; if there are no remaining foxes or the model has run for 200 years, then the simulation will stop. Fig. 5 shows how each procedure leads to the next within this model.

3.2 Design Concepts

3.2.1 Basic Principles

The basic principle of this simulation is to replicate Santa Cruz island fox dynamics in the presence of golden eagle predation. With 10 golden eagles and an initial population size of 1464 foxes, we observe similar dynamics to those seen in the early 1990s (Coonan, 2003). The number of eagles initially present and preying on island foxes is based on verified nests on the island (Collins and Latta, 2006). We model eagle feeding habits and diet composition using data collected from nest excavations (Collins and Latta, 2006). The fox populations reproduce and behave realistically based on data collected through behavioral and ecological field studies (Coonan, 2003; Moore and Collins, 1995; Roemer et al., 2001; Scott et al., 2014; Vissman, 2004).

3.2.2 Emergence

When golden eagle predation is not included in this model and there is an initial population of 40 male foxes and 40 female foxes, we see the emergence of logistic growth with a carrying capacity around 1440 (see Section 4.1.1). This is similar to the population size observed in 1994 (see Fig. 2) (Coonan, 2003).

3.2.3 Adaptation

Male and female foxes determine the size of their territory based on surrounding vegetation (Vissman, 2004). The smaller territory radius is 0.36 km, while the larger territory radius is 0.87 km (Vissman, 2004). If mated foxes are within an area that is more than 30% grassland, then they will create the larger territory size, if not, they will create the smaller territory size (Vissman, 2004). In the model, foxes have a limited attempts to find an unoccupied, habitable territory within the boundaries of the island. For details, see MAKE-FOX-TERRITORY submodel in Section 3.3.2. In this way, as the island becomes more crowded, the territory sizes become smaller and the chances of finding a suitable territory within the allotted trials decrease. If a fox mated pair is unable to find a suitable territory within the five allotted trials, then they will break their mated pair and

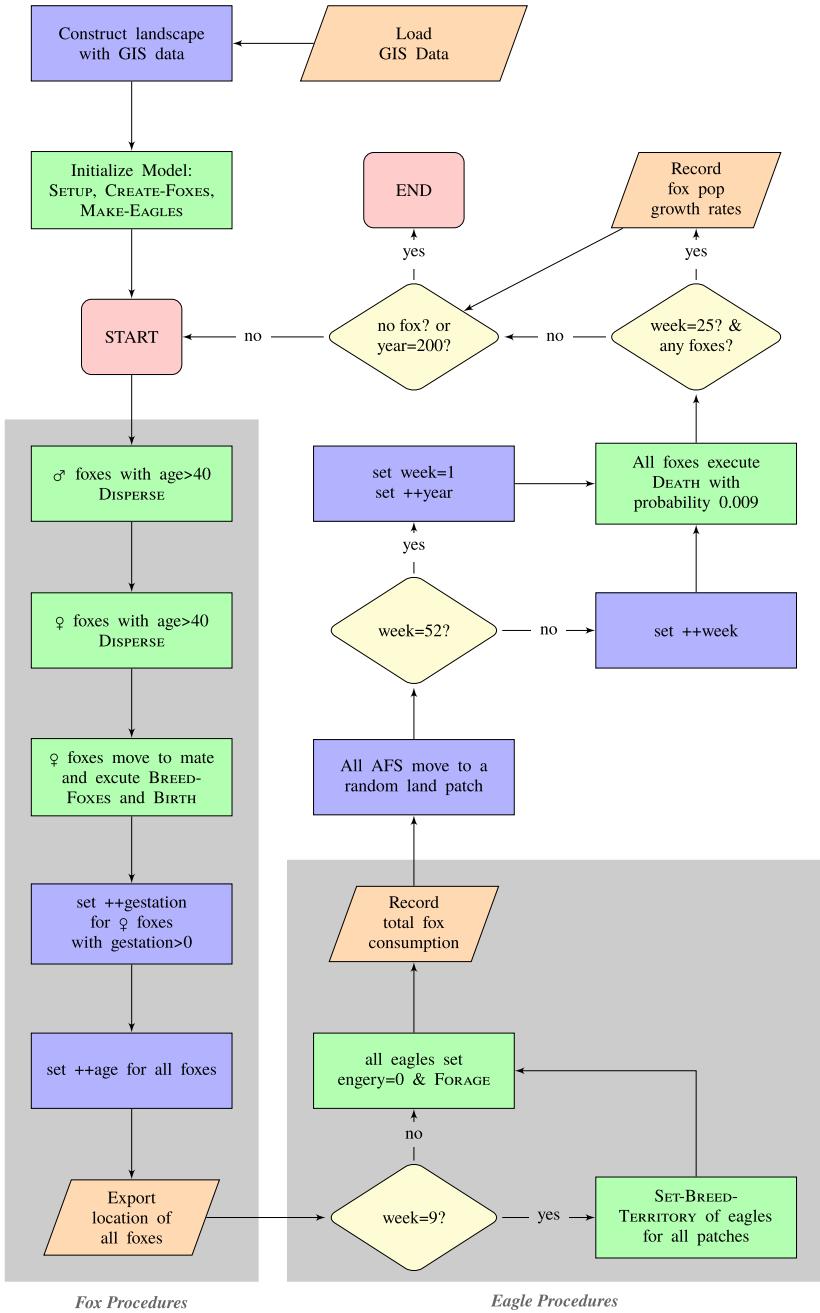


FIG. 5 Flow diagram of the model. Procedures in green represent specific submodels (see Section 3.3.2). The loop represents the order of procedures during the execution of one time step.

attempt to mate with other individuals. After the birth of fox pups, foxes will not move from their natal territory until they are of reproductive age (40 weeks). If there are no available territories due to high fox population densities, fox pups may remain in their natal territories their entire lives, even after reaching reproductive age (Coonan, 2003).

3.2.4 Objectives

The objective of a fox is to mate and successfully reproduce. Their territory decisions are based on the vegetation around them. Mating decisions depend on availability of mates and whether they are of reproductive age and are unmated. An eagle's objective is to reach their weekly energy requirements within the number of allowed trials. The AFS have no objectives in this model.

3.2.5 Learning

The foxes, eagles, and AFS have no learning capacity in this model.

3.2.6 Prediction

The foxes, eagles, and AFS have no predictive capacity in this model.

3.2.7 Sensing

Foxes can sense the age, gender, and mated-status of foxes within their search radius, which directs movement and mating. They can also sense whether patches are occupied by other foxes and the vegetation type there. Foxes can sense breeding season (weeks 7–12) and will attempt to reproduce if they are mated (Moore and Collins, 1995). Eagles sense their own breeding season (weeks 9–32) and whether patches are within their hunting or breeding territories (Todd, 2000).

3.2.8 Interaction

Male and female foxes interact to establish mated pairs and to form territories on the island. Foxes and eagles have an antagonistic interaction when the eagles hunt and feed. Eagles and AFS have a similar antagonistic interaction. Foxes and AFS have no interaction.

3.2.9 Stochasticity

Within this system, there are many processes dependent upon stochastic decisions. Whenever a set of entities (agents or patches) executes a command or procedure, the order in which each entity within the set are selected to execute the task is randomized. Additionally, there are many decisions made by the agents or patches which are stochastic. Within the framework of the NetLogo software, stochastic decisions by entities are determined by random number generation or random selection of an agent or patch from a set of entities with equal probability.

3.2.9.1 Decisions Using Random Number Generation

Let X be a decision that occurs in the model with probability P , and does not occur with probability $1 - P$. Each time decision X is to be made, we sample the uniform distribution $\mathcal{U}[0, 1]$ to generate the value $y \in \mathbb{R}$; the event X occurs if $y \leq p$, and does not occur otherwise. Here, we provide the specific probabilities used for stochastic model decisions.

- Each fox pair that is not currently gestating offspring will successfully reproduce with probability $p = 0.61$ in a given time step during the fox breeding season (weeks 7–12) (Scott et al., 2014).
- At each time step each fox will die naturally with probability $p = 0.009$ (Scott et al., 2014).
- The number of offspring born to any pregnant female fox is one with $p_1 = 0.558$, two with $p_2 = 0.356$, and three with $p_3 = 0.086$ (note $p_1 + p_2 + p_3 = 1$) (Coonan, 2003). In this case given the value y sampled from the uniform distribution $\mathcal{U}[0, 1]$, the pregnant female fox will produce a litter of

$$\begin{cases} 1 \text{ pup} & \text{if } y \leq p_1 \\ 2 \text{ pups} & \text{if } p_1 > y \leq p_1 + p_2 \\ 3 \text{ pups} & \text{if } y > p_1 + p_2 \end{cases}$$

Other stochastic events require sampling from uniform distributions over wider or smaller ranges.

- Upon the creation or birth of each fox it is given a randomly generated mass. The mass is sampled from the uniform distribution $\mathcal{U}[1.200, 2.700]$ kg for male foxes and $\mathcal{U}[1.070, 2.722]$ kg for female foxes (Moore and Collins, 1995).
- Each eagle has an individual preference for choosing a fox as its prey over an AFS (when both are present within its territory). For each eagle this preference value is sampled (during initialization) from the uniform distribution $\mathcal{U}[0.457, 0.577]$ (Collins and Latta, 2009).

3.2.9.2 Decisions Using Random Selection of Entities

When entities (agents and patches) interact, typically one entity is stochastically selecting the entity or subset of entities with whom it will interact. The selecting entity makes its selection randomly from a group where each entity within the group has an equal probability of being selected. Here, we provide the details on who the selecting entities are and from which group of entities they are selecting.

- When mating, each fox chooses an individual of the opposite sex and of reproductive age randomly from within their search radius (see MAKE-FOX-TERRITORY submodel in Section 3.3.2).
- At each breeding season, the eagles randomly choose which nest to occupy for that year.

- In the case where breeding territories of two eagles overlap (see Fig. 7), the eagle pair that gets use of the shared space is chosen randomly.
- When an eagle is foraging, if foxes are present, the eagle selects a fox at random from within its territory with probability equal to the eagle's individual preference for choosing a fox as its prey; otherwise the eagle selects an AFS at random from within its territory (see FORAGE submodel in Section 3.3.2). Note, the eagle's territory is restricted to its breeding territory during breeding season (weeks 9–32).
- Each time step the AFS move to a randomly selected land patch (see DISTRIBUTE-FOOD submodel in Section 3.3.2).
- If a fox is unable to find a mate (see the DISPERSER submodel in Section 3.3.2), the fox will move to a randomly selected patch within its search radius that is a land patch and does not contain a fox of the opposite sex.

3.2.10 Collectives

The collectives of this model include the mated pairs of female and male foxes. Once fox pups are birthed, they will remain in their natal territory and add to the collective until they are of reproductive age and can establish their own territory. Eagles are also in mated pairs and forage only within their hunting or breeding territories, which are shared with a mate. AFS do not form collectives.

3.2.11 Observation

At each time step, we record the fox population size, the number of foxes consumed, the current week, and the current year. At week 25 of each year, we record the per capita growth rate over the previous year as well as the per capita growth rate from the initial population size (see Scott et al. (2014) for associated formulas). We also record the total fox population and the number of eagles feeding on foxes each week.

3.3 Details

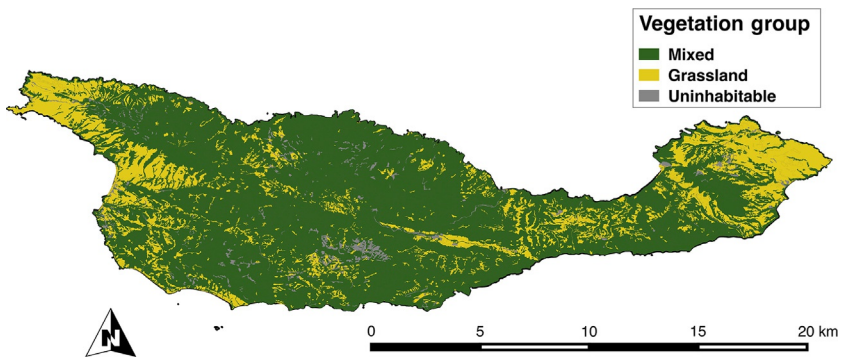
3.3.1 Initialization

A data set giving the spatial distribution of vegetation types on SCI is used to define the patch variables of `vegetation-type` and `vegetation-group`, and to determine if a patch is land or water (Cohen et al., 2009). Table 1 and Fig. 6 show the vegetation composition and distribution of SCI. Location data were rectified onto an SCI map and used to define the five golden eagle hunting territories and eagle nest locations (Collins and Latta, 2009). Eagle breeding territories were defined with 25 km² buffer regions around each nest location (Todd, 2000). This GIS data set is used to define eagle hunting and breeding territories.

During the setup procedure, global variables are initialized, all GIS data sets are loaded, and corresponding patch variables defined. An initial fox

TABLE 1 SCI Composition by Vegetation Type and Group
(Cohen et al., 2009)

Vegetation Type	% of Patches	Vegetation Group	% of Patches
Fennel	1.4	Grassland	41.2
Herbaceous	39.8		
Deciduous	18.0	Mixed	58.2
Evergreen	27.5		
Forest-conifer	3.3		
Forest-nonconifer	9.4		
Sparse	0.1	Uninhabitable	0.6
Other	0.5		

**FIG. 6** Vegetation map of SCI. In yellow is grassland where fox territory size is larger. In dark green is mixed vegetation where fox territory is smaller. In gray is uninhabitable vegetation where foxes cannot form territories (Cohen et al., 2009).

population is generated with an even sex ratio and the initial age of each fox is drawn from a uniform distribution over the range [0,312] weeks (note 312 weeks is ~ 6 years) (Coonan, 2003). The initial fox population is randomly distributed over the island, a pair of eagles is placed on within each golden eagle hunting territory (a total of 10 eagles), and the AFS are distributed across the island (see the DISTRIBUTE-FOOD submodel in Section 3.3.2). If there exists a suitable mate for a fox, they will form a mated pair and make a territory. The territory size of each mated pair is dependent upon the vegetation they inhabit (see MAKE-FOX-TERRITORY submodel in Section 3.3.2 for details) (Coonan, 2003).

3.3.2 Submodels

The various submodels of the ABM are described here in detail. Note, submodels are also referred to as *procedures* through the ODD description. The italicized text in each procedure's description identifies which set of entities executes the procedure. When a set of entities executes a procedure, the order in which each entity of the set is selected to execute the procedure is random.

FORAGE

This procedure is executed by eagles. First, eagles set their hunting trials to zero. Until they have reached their required weekly energy level and while they have remaining trials (of the allotted 7), eagles will look for prey in their hunting territory. During eagle breeding season (weeks 9–32), eagle hunting territory is limited to one of the breeding territories, which surround a randomly chosen nest (Collins and Latta, 2006). If there are any foxes within the hunting territory, then the eagles will consume one of the foxes within its territory. This occurs with a probability defined by the eagle's variable of their preference for eating foxes ($p \in [0.457, 0.577]$). If the eagle does not feed on a fox, it will randomly select an AFS within their territory. Once the eagle has selected its prey, it increments its energy by the mass of the fox or AFS selected. If a fox was consumed, the global number of foxes consumed is incremented by one and the eagle sets the Boolean variable determining that they have consumed a fox in that time step to "true." If there are no foxes in the eagle's territory, then the eagle will randomly select an AFS within their hunting territory and increment its energy by the energy of the AFS. The amount of energy obtained from each prey type is determined by the weight of each prey (see Table 2). The eagle will set its `trials` variable equal to zero after successful foraging. If there are no AFS or foxes in the eagle's territory, it will increment its trials by one. If the `energy` variable of the eagle is still below 1.68 kg of food and the `trials` variable of the eagle is still below 7, the eagle will make another attempt to forage.

DISPERSE

This procedure is executed by male and female foxes of reproductive age. If there are any unmated foxes of reproductive age and of the opposite sex within the executing fox's search radius, then a mated pair will be created and the male will attempt to form a territory (see the MAKE-FOX-TERRITORY procedure). If there are no unmated foxes of reproductive age and the opposite sex in the search radius, then the fox will randomly move to one of the island patches within its search radius that has no foxes of the opposite sex.

MAKE-FOX-TERRITORY

This procedure is executed by newly mated males. The large and small fox territory sizes are set to 0.87 km^2 and 0.36 km^2 , respectively (Vissman, 2004).

TABLE 2 Composition of a Golden Eagle's Diet

Common Name	Avg. Individual Weight (kg)	% of Eagle Diet
Deer mouse	0.020	0.15
Western spotted skunk	0.560	1.04
European mouflon sheep	2.300	12.77
Double-crested/Brandt's cormorant	1.962	29.05
Herring gull	1.135	4.20
California gull	0.607	2.25
Western/glaucous-winged gull	0.875	21.05
California quail	0.173	0.64
Common raven	1.199	28.85

The original data comes from a study which excavated four golden eagle nests on SCI to determine the species of discarded remains (Collins and Latta, 2006). For our model, only mammalian and bird species were included as only trace amounts of fish, invertebrate, and crustacean remains were found in the excavated nests.

Then, the fox's territory size is initially set to the smaller territory centered at the fox's current location. Next, the `percent-grassland` variable is set as the number of land patches within the fox's territory radius that have `vegetation-group grassland` divided by the total number of patches within this radius, that is

$$\text{percent-grassland} = \frac{\# \text{ of grassland patches in territory}}{\text{territory size}}.$$

If `percent-grassland` $< 30\%$, then the fox's territory remains as the small territory size, however if `percent-grassland` $\geq 30\%$, then the fox's territory size will change to the larger territory size. Next, the fox initializes its number of trials to establish a territory with its mate to 0. The fox then searches for a viable territory until he either establishes a suitable territory or reaches five trials.

While there are any unsatisfactory patches (patches that are occupied or of uninhabitable vegetation) within the male fox territory, the male fox will try to find a suitable territory. He will change his territory size by a small factor with each successive attempt. The specifics of the territory trial process are as follows: if there are any land patches within his territory size that are unoccupied, he will randomly move to one of those patches, increase his number of trials by 0.4 and multiply his territory size by a factor of 0.98. If there are no unoccupied, land patches within the male territory, he will randomly move to one of the patches in his territory size, increment his territory trials by 1, and

multiply his territory size by a factor of 0.95. Note, depending on how densely populated the island is with foxes, the male fox may have between 5 and 12 trials to establish a territory; the more densely populated the island the fewer trials the fox is likely to have. In this way, when there are still viable patches, foxes have more attempts to decrease their territory size slightly in order to find a suitable territory.

Once the male fox has a set his territory, he checks to be sure the territory has at least 45 land patches (0.2205 km^2 , a lower bound on territory size). If so, then he is successful in forming a territory and will set his Boolean `territorial?` variable to “true” and will set the owner of the patches within his territory to his ID number. Additionally, he will set his mate’s Boolean `territorial?` variable to “true” and define her territory size as the same as his. In the case where a territory cannot be made, the male fox will set his `territorial?` variable to “false”, break his mated pair, and the male fox will move to a random location on the island.

SET-EAGLE-BREEDING-TERRITORIES

This procedure is not executed by any entities; instead it is called by the main procedure at week 9 each year (i.e., once every 52 time steps). Note, there are five different eagle territories: Christy’s Watertank (CW), Coche Point (CP), Lady’s Harbor (LH), Laguna (La), and Red Peaks (RP) (Collins and Latta, 2006). The locations of the eagle territories and eyrie locations are accessed through imported GIS data (see Fig. 1) into the model during initialization (Collins and Latta, 2006). Each patch in the landscape has Boolean variables `CW-BT?`, `CP-BT?`, `LH-BT?`, `La-BT?`, and `RP-BT?`, which will be set to “true” when that patch is a part of the associated breeding territory for that year’s breeding season. At the beginning of this procedure, all five of these Boolean variables are set to “false”. Next, one nest for each mated eagle pair is chosen; this will be the center of each pair’s breeding territory for the current breeding season. Using the imported GIS data, the appropriate Boolean variables are set to “true” to indicate which patches are a part of each pair’s breeding territory for this breeding season. Depending on which eyrie locations were randomly chosen, there may be overlap between (1) Christy’s Watertank and Lady’s Harbor, (2) Lady’s Harbor and Red Peaks, (3) Christy’s Watertank and Laguna, and (4) Laguna and Red Peaks; see Fig. 7 for an example of one selection of breeding territories showing the potential overlaps (1) and (4). If any two breeding territories overlap, one of the territories is randomly chosen to occupy the overlapping area for the current breeding season.

BREED-FOXES

This procedure is executed by female foxes. If a female fox is of reproductive age (>40 weeks old), not already pregnant, is part of a territorial mated pair, and it is between weeks 7 and 12 of the current model year, then the female

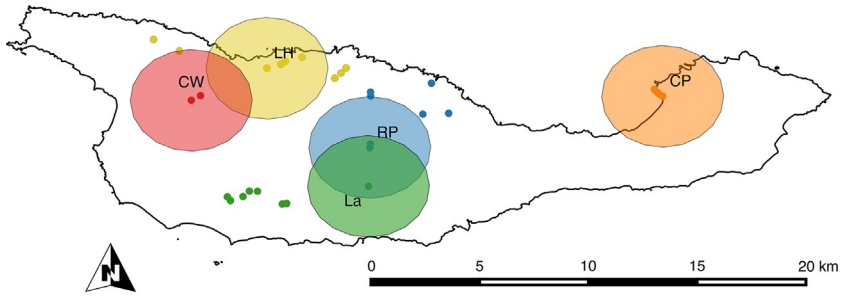


FIG. 7 An example of breeding territories for the five eagle pairs: Christy's Watertank (CW, red), Coche Point (CP, orange), Lady's Harbor (LH, yellow), Laguna (La, green), and Red Peaks (RP, blue) (Collins and Latta, 2006). The Eyrie locations are shown as points in corresponding colors.

fox will conceive a litter with probability $p = 0.61$ (i.e., there is a 61% chance of successful reproduction) (Sanchez and Hudgens, 2011).

BIRTH

This procedure is executed by female foxes. If the gestation period of a female fox has reached 7 weeks, she gives birth. The number of offspring born is randomly chosen with a 55.8% chance of producing 1 offspring, a 35.6% chance of producing 2 offspring, and a 8.6% chance of producing 3 offspring (Coonan, 2003). Next, male and female foxes of the mated pair increment their numbers of progeny by the number of offspring birthed. Male and female fox pups are produced with an equal chance due to an even sex ratio (Coonan, 2003). The offspring's age is set to zero, gestation (if female) is set to zero, Boolean variable `territorial?` is set to "false" indicating the pups have not created a mated pair and established territory yet, and mass (or energy) is set to random value in the range [1.200, 2.700] kg if male and [1.070, 2.722] kg if female. Lastly, the mother female fox resets her gestation to zero (Moore and Collins, 1995).

DEATH

This procedure is executed by foxes at random with probability 0.009 (the natural death rate) (Scott et al., 2014). Any patches within the territory of the dead fox will be reset to have no owner. If the dead fox has a mate, the link establishing the mated pair will be broken and the mate's Boolean `territorial?` variable will be set to "false" (allowing the widowed fox to find a new mate).

DISTRIBUTE-FOOD

This procedure is called by the setup procedure during initialization. Based on prey remains collected from eleven golden eagle nests on the Channel Islands and using the *matrix* extension in NetLogo, we develop a matrix of a typical SCI golden eagle's diet composition (see Table 2) (Collins and Latta, 2009;

Wilensky, 1999). There are nine main species within Channel Island eagle diets, excluding foxes. We determine eagle diet composition based on island biomass; SCI biomass is 152.172 kg with SCI foxes and 144.028 kg without SCI foxes (Collins and Latta, 2006). The model creates the number of each AFS based on the percentage of the overall biomass (without foxes) each species composes. Each AFS is also given an average amount of energy (equal to its mass in kg) an eagle will gain from consumption based on the fresh weight of the species (Collins and Latta, 2006).

4 RESULTS

In the following sections, we show the results of the fox population dynamics with and without the inclusion of golden eagle predation.

4.1 Results of Model Analysis Without Golden Eagle Predation

4.1.1 SCI Fox Carrying Capacity

Starting with 40 female and 40 male foxes of varying ages distributed randomly across the island, we simulated the SCI fox population dynamics over 200 years without eagle predation. This simulation experiment was repeated 100 times to capture the range in population dynamics due to model stochasticity. For each simulation the size of the population was recorded at week 25 each year after the fox breeding season. The mean and standard deviation in population size were calculated for each year over all 100 simulations and are shown as the gray curve and shaded region, respectively, in Fig. 8. For each of the 100 simulations, the population increases to a carrying capacity near the 1465 carrying capacity estimated

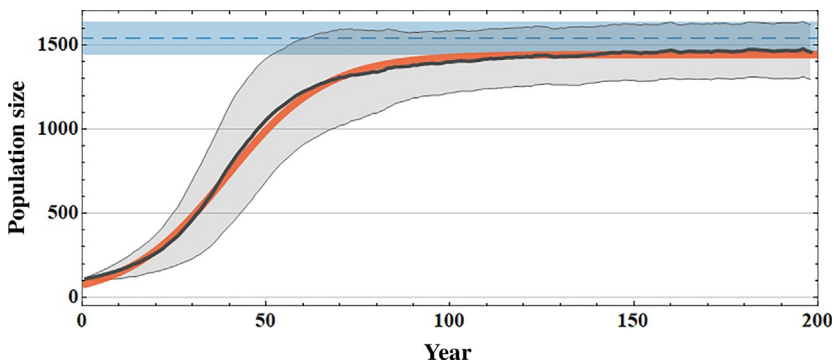


FIG. 8 This graph plots the average population size over 200 years. The blue horizontal region is the carrying capacity for the island as estimated by Coonan (2003) with the dashed line at 1465. The thick *gray line* represents the mean population size of 100 simulated populations. The surrounding *gray region* represents ± 1 standard deviation of the mean population size over 100 simulations. The thick *orange line* is the logistic growth curve fitting Eq. (1).

in 1993 (see the dashed blue line) (Coonan, 2003). The simulated SCI fox population size over time can be approximated by a logistic growth curve with the equation:

$$N(t) = \frac{KN_0e^{rt}}{K + N_0(e^{rt} - 1)}, \quad (1)$$

where $N(t)$ is the SCI fox population size at year t with $N_0 = N(0)$ (the initial population size), r is the intrinsic growth rate, and K is the carrying capacity (Edelstein-Keshet, 2005). For the simulated 100 SCI fox populations, $N_0 = 80$ since each simulation started with 80 foxes. Using the `FindFit` function in Wolfram Mathematica (Wolfram Research, 2010) the logistic growth curve parameters for the SCI fox population are estimated to be $K = 1442.33$ ($p < 0.01$) and $r = 0.07400$ ($p < 0.01$).

4.1.2 SCI Fox Population Viability

The model simulations to determine carrying capacity all started with the same population size: 80 foxes. However, because previous modeling had shown the emergence of an Allee effect which led to population decline at low population size, we next tested the population viability of the SCI foxes by beginning with varying initial fox population sizes, always with an even sex ratio (Scott et al., 2014). Starting with an initial population of x foxes, we ran 100 simulations until either the fox population was extinct or the population had grown to $\frac{1}{2}K$ (where $K = 1442.33$ as estimated from the previous analysis, see Fig. 8). For each set of 100 simulations we calculated the proportion of simulations where the population survived to $\frac{1}{2}K$. This calculation was repeated for each initial population size x . We found that the viability of island foxes (in the absence of golden eagle predation) increased as initial population size increased according to a Holling type III functional response curve (Kot, 2001). The probability of reaching $\frac{1}{2}K$ is given by:

$$P\left(\text{reach } \frac{K}{2} \mid N_0 = x\right) = \frac{\alpha x^n}{1 + \alpha x^n}. \quad (2)$$

Using the `FindFit` function in Wolfram Mathematica and the simulated data, the functional response curve parameters were estimated as $n = 3.545$ and $\alpha = 7.53 \times 10^{-6}$, fitting the model with standard error of 0.0344 (Wolfram Research, 2010). The simulated data and parameterized functional response curve are shown in Fig. 9. Given the parameterized model, $P(\text{reach } K/2 \mid N_0 = x) = 0.99$ when $x = 102$. Thus, once the initial population size is at least 102 foxes, we would expect, with a 99% probability, that the population would grow to at least half-carrying capacity. Presumably, once the population has reached half-carrying capacity it will be able to continue to grow toward carrying capacity, though the speed at which the population is growing would slow (assuming logistic growth dynamics).

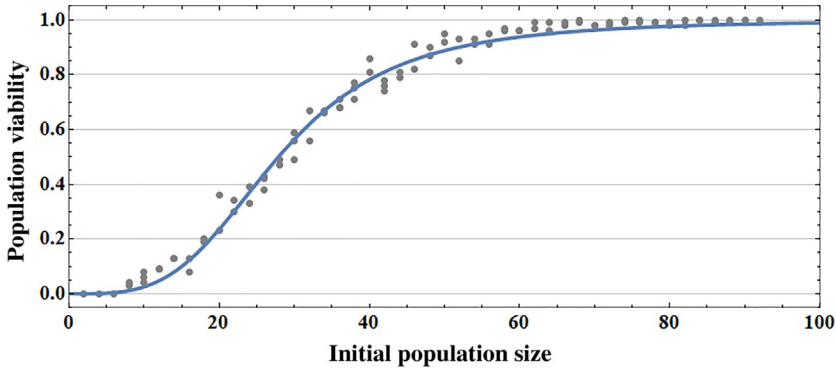


FIG. 9 Population viability based on varying initial population sizes. Each data point represents the proportion of 100 simulations, starting with x foxes, that survived to reach $K/2$ (half of carrying capacity, ~ 721 foxes, as seen in Fig. 8). The blue curve represents Eq. (2) with $n = 3.545$, and $\alpha = 7.53 \times 10^{-6}$.

4.1.3 SCI Fox Spatial Distribution

After running simulations, we also mapped spatial data of fox locations onto GIS maps to show the impact of including vegetation data (see Fig. 6 for vegetation distribution). SCI fox territory size depends on the local composition of vegetation, with smaller territories occurring in the mixed vegetation areas, while larger territories occur in areas with grassland vegetation. Larger territories therefore occupy the outer edges, with smaller territories toward the island's center.

Fig. 10 maps this density over time (1–130 years) without golden eagle predation, as predicted by our model, when starting with an initial population size of 80 foxes (40 male, 40 female). The location (using CRS NAD83 for North America; EPSG:4269 coordinates) of each fox in the simulation is recorded at week 25 each year. We then map each fox onto SCI and use the heatmap function of QGIS to observe the change in density over time. This QGIS plugin uses kernel density estimation to estimate the fox density values at every point on the island. Kernel density estimation is a nonparametric density estimator that smooths the contribution of each observed data point over a local neighborhood of that individual data point. The contribution of data point x_i to the estimate at x^* depends on the distance between x_i and x^* (Bozdogan, 2018). The QGIS kernel density estimation plugin uses a quartic kernel in order to estimate density. To create the heatmaps in Figs. 10 and 12, we use a radius of 2000 m, giving an area of $\sim 12.57 \text{ km}^2$. Therefore, if the density value at a certain point is 12.57 foxes, there is one fox per km^2 in that location. The legend in Figs. 10 and 12 has been rescaled in terms of foxes per km^2 for ease of interpretation.

Fig. 10 shows that without predation pressure, the island fox population forms more dense populations in the center of the island, consistent with the

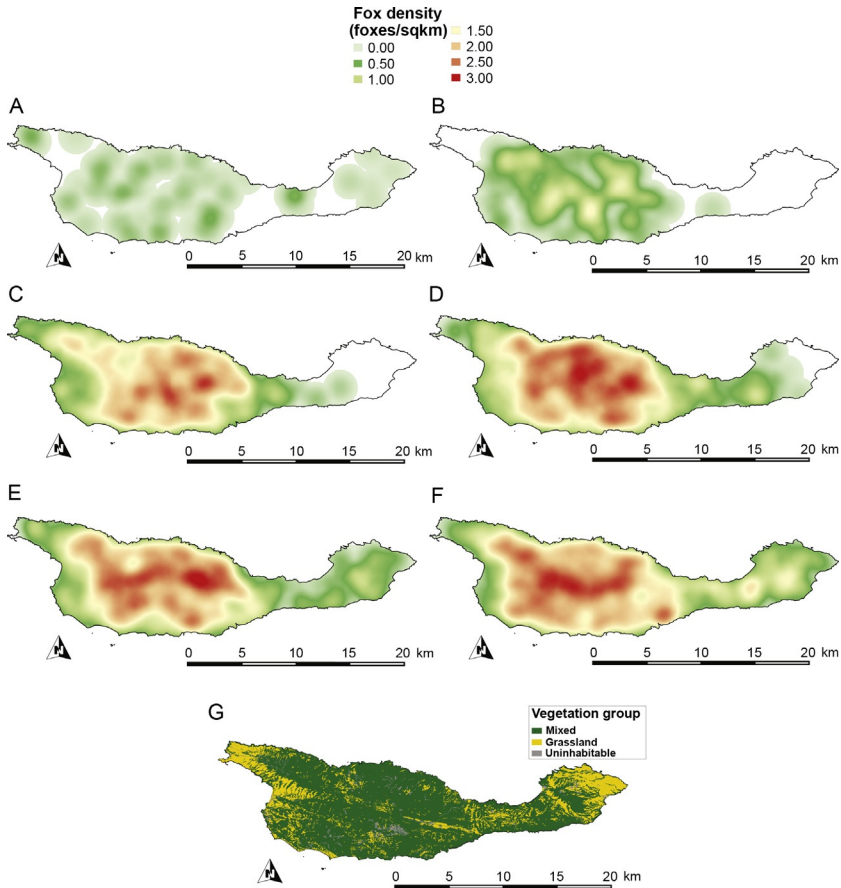


FIG. 10 These figures represent the density of foxes without predation on SCI at years 1 (A), 25 (B), 50 (C), 75 (D), 100 (E), and 130 (F). The *red* areas represent regions of high fox density, the *yellow* areas represent regions of medium fox density, and the *green* areas represent regions of low fox density; *white* regions have no foxes. The vegetation group map from Fig. 6 is shown in (G) for comparison of vegetation distribution and fox distribution.

vegetation. As time continues and population size grows, the island fox population spreads to cover the island, but the highest density regions remain in the island's center where mixed vegetation allows for smaller territory sizes and thus greater density.

4.2 Model Results with Golden Eagle Predation

We also simulated the SCI fox population with golden eagle predation. At each time step, we took a measure of the number of island foxes present on

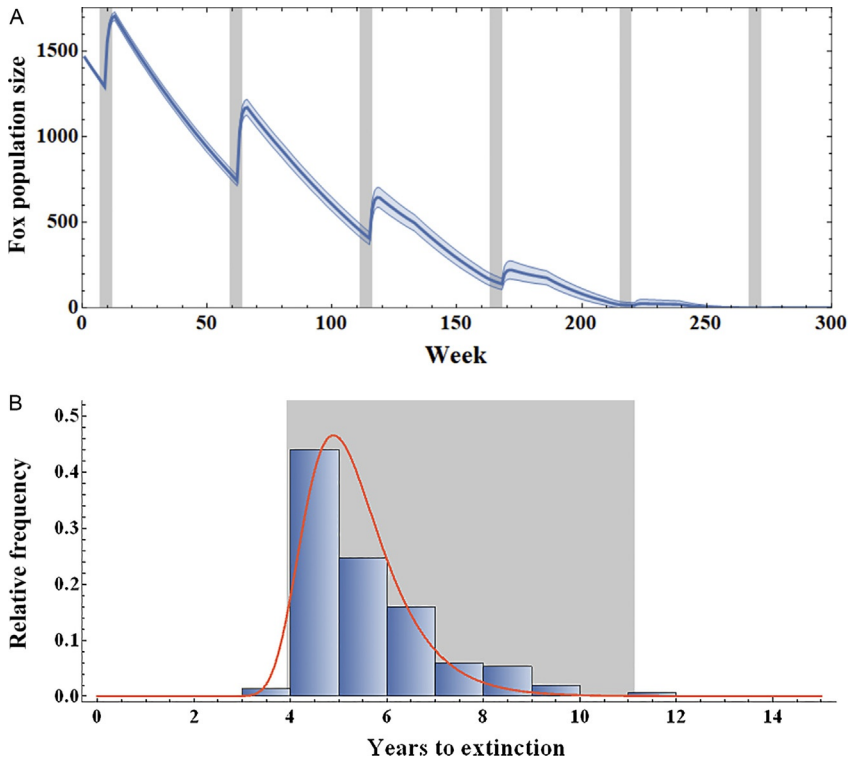


FIG. 11 (A) The average population size of SCI foxes at each time step over 150 simulations with the influence of golden eagle predation. The *gray* regions represent fox breeding season (weeks 9–12); the *shaded blue* region around the curve shows ± 1 standard deviation from the mean. (B) A histogram of the time to fox population extinction over 150 simulations; the full range of the years to extinction is shown by the *gray shading*. The data are fit with an extreme value distribution curve given by Eq. (3) where $\alpha = 4.89$ and $\beta = 0.791$.

the island. The population declined steadily, but during fox breeding season, there were spikes in population size. Fig. 11A shows the fox population size over time with golden eagle predation averaged over 150 simulations. Note that Fig. 11A shows simulations from weeks 1–300 even though 45 of the 150 simulations had nonzero population sizes after week 300. However, the maximum fox population size over all 150 simulations at week 301 was 7 foxes.

We additionally determined the average number of years a fox population could subsist on SCI under the influence of golden eagle predation. Using the same 150 simulations, we recorded the first time step at which the fox population size dropped below 1 fox. The weeks to extinction were then scaled to years to extinction and plotted in a histogram shown in Fig. 11B. The mean number of years to fox extinction is 5.40, the median is 5.02 years, and the

standard deviation is 1.25 years. The distribution for the years to extinction can be approximated by an extreme value distribution (EVD) (Hosking et al., 1985) given by equation

$$P(x) = \exp\left(\frac{\alpha-x}{\beta} - \exp\left(\frac{\alpha-x}{\beta}\right)\right), \quad (3)$$

where $\alpha = 4.89$ and $\beta = 0.791$. Given the null hypothesis that the years to extinction data is fit by the extreme value distribution with $\alpha = 4.89$ and $\beta = 0.791$ and an acceptance level of $p = 0.001$, the null hypothesis is rejected by the Pearson χ^2 test ($p \ll 0.001$), but accepted by the Anderson–Darling test ($p = 0.0064$) and the Cramer–von Mises test ($p = 0.0074$).

Using the same procedure from Fig. 10, we map the spatial distribution of the fox population under eagle predation for three separate simulations, shown in Fig. 12. We then create a time-lapse video of the SCI fox distribution over the length of the three simulations. Each frame in the video contains three SCI fox distribution heat maps (one for each simulation) generated for one time step (1 week) in the model. The Video clip 1 <https://doi.org/10.1016/bs.host.2018.10.001> is available in the Supplementary Material. For the first years of the simulations, fox breeding season allows the population to partially rebound during the fox breeding season following eagle

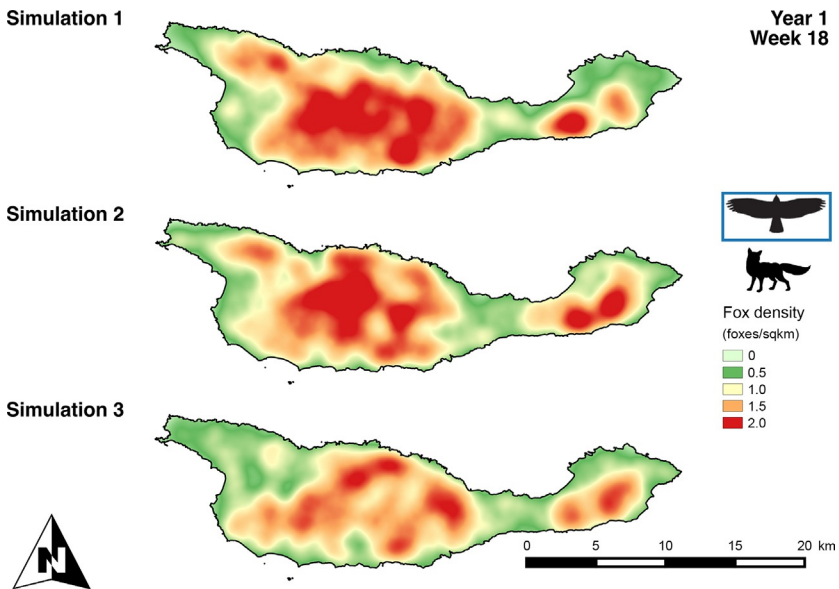


FIG. 12 Three separate simulations showing the spatial distribution of foxes under golden eagle predation. During the breeding season of each species, the icon on the right is highlighted to indicate changes in behavior or dynamics.

predation. As the fox population size becomes smaller, the number of pups added after breeding season does not replenish those lost to predation. Additionally, the spatial distribution of the foxes changes over time. Early in the simulation there is higher fox density in the center of the island. As the population is subject to predation, the foxes are distributed to the outer edges of the island. In all three of the simulations shown in the time-lapse, the last remaining foxes have territories on the edges of the island.

5 CONCLUSIONS AND DISCUSSION

From the above results, we draw the following conclusions. First, in analyzing our model without the presence of golden eagle predation, we see that our model correctly predicts variable SCI fox territory size based on vegetation type. On the outer edges of the island where larger territories form due to grassland habitats, we see lower fox densities. Conversely, in the island's center where there are areas of mixed vegetation, we see higher fox densities. Additionally, while our model does not explicitly include a carrying capacity for the SCI fox population, due to our inclusion of fox behavior decisions regarding the establishment of territories and the inclusion of vegetation data for SCI, our model closely predicts the SCI fox carrying capacity estimated by previous research and field data (Coonan, 2003; Scott et al., 2014).

Furthermore, we also show this ABM model can produce logarithmic growth of the fox population when the population size is recorded yearly thus ignoring the temporal dynamics of the birth pulse. A population starting with 80 foxes (40 male, 40 female) will reach half-carrying capacity between 40 and 50 years later (see Fig. 8). Reaching half-carrying capacity always ensured survival to carrying capacity according to our analysis of SCI fox population viability. In fact, our results show that an SCI fox population starting with slightly more than 100 foxes (with an even sex ratio) all but guarantees survival to half-carrying capacity, and then to carrying capacity after that.

Population viability analysis allow us to determine the minimum population size that will produce carrying capacity, if the population is unadulterated by golden eagle predation or other population decline factors (see Fig. 9). Similarly, if our GIS maps and data are correct, we can pinpoint locations on the island where we would expect foxes to exist at high densities and low densities, as well as eagle nest proximities to fox populations (see Fig. 10).

Under the predation of 10 golden eagles comprising 5 mated pairs, our model predicted the SCI fox population to experience a rapid decline. It took the eagles around 5 years to eradicate the fox population ($\mu = 5.41$). This concurs with data collected on the SCI fox population in the 1990s–2000s. From 1994 to 1999 (a 5-year span), the SCI fox population fell from 1465 to 135 foxes, by 2004 (10 years later) the fox population reached a low of 89 foxes. Based on results from our model, while there is a 58% chance the SCI fox population would have survived more than 5 years before going extinct, there

is less than a 1% chance that the SCI fox population would have survived more 9 years before going extinct. This indicates that the SCI fox population was either very “lucky” or other factors like intensified surveillance of the SCI foxes and the beginnings of conservation measures helped ensure their survival in otherwise unfavorable circumstances. The conservation efforts of the National Park Service and Nature Conservancy were therefore fortuitous.

From the number of years to extinction, we can determine the average number of years that the fox population can exist before going extinct in the absence of conservation efforts (see Fig. 11). There is a significant drop in fox consumption during eagle breeding season, meaning conservation efforts may be more successful during this time, when there is less of a threat of eagle predation.

The research presented here shows the fragility of island populations and the utility of including carefully curated GIS data in agent-based models used to study such fragile populations. Using models similar to this, we can improve the predictive capacity of conservation efforts on the Channel Islands and in other regions of isolated populations.

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APPENDIX

Supplemental Resources

The authors have provided the model code (in NetLogo) and associated GIS data files which are imported into the model. Additionally, a video clip of the SCI fox population density under golden eagle predation for three simulated fox populations (referenced in Fig. 12) is provided. The model code, data files, and [Video clip 1 https://doi.org/10.1016/bs.host.2018.10.001](https://doi.org/10.1016/bs.host.2018.10.001) are available in the Supplementary Material online.

REFERENCES

- Bakker, V.J., Garcelon, D.K., Aschehoug, E.T., Crooks, K.R., Newman, C., Schmidt, G.A., Van Vuren, D.H., Woodroffe, R., 2003. Current status of the Santa Cruz island fox (*Urocyon littoralis santacruzae*). In: 6th California Islands Symposium.
- Bonabeau, E., 2002. Agent-based modeling: methods and techniques for simulating human systems. *Proc. Natl. Acad. Sci.* 99 (suppl 3), 7280–7287.
- Bozdogan, H., 2018. Modern statistical theory and inference: an informational modeling process with Matlab. (in preparation).
- Cannata, N., Corradini, F., Merelli, E., Tesi, L., 2013. Agent-based models of cellular systems. *Methods Mol. Biol.* 930, 399–426.

- Clark, H.O., 2009. Species at risk: golden eagle predation on arid-land foxes. *Endangered Species Update* 26 (1 & 2), 10–14.
- Cohen, B., Corry, C., Menke, J., Hepburn, A., 2009. A spatial database of Santa Cruz island vegetation. In: *Proceedings of the 7th California Islands Symposium*.
- Collins, P.W., 1991. Interaction between island foxes *Urocyon littoralis* and Indians on islands off the coast of Southern California. *J. Ethnobiol.* 11 (1), 51–81.
- Collins, P.W., Latta, B.C., 2006. Nesting Season Diet of Golden Eagles on Santa Cruz and Santa Rosa Islands, Santa Barbara County, California. Santa Barbara Museum of Natural History. Technical Reports No. 3.
- Collins, P.W., Latta, B.C., 2009. Food habits of nesting golden eagles *Aquila chrysaetos* on Santa Cruz and Santa Rosa Islands, California. In: *Proceedings of the 7th California Islands Symposium*.
- Conner, M.M., Ebinger, M.R., Knowlton, F.F., 2008. Evaluating coyote management strategies using a spatially explicit, individual-based, socially structured population model. *Ecol. Model.* 219 (1), 234–247.
- Coonan, T.J., 2003. Recovery Strategy for Island Foxes on the Northern Channel Islands. National Park Service: Channel Islands National Park.
- Coonan, T.J., 2008. Island Fox Captive Breeding Program: 2007 Annual Report. National Parks Service: Channel Islands National Park, Ventura, CA. 08-01.
- Coonan, T.J., 2009. Eleventh Annual Meeting: Island Fox Working Group. National Parks Service, Sheraton Four Points Hotel, Ventura, CA.
- Coonan, T.J., 2010. Twelfth Annual Meeting: Island Fox Working Group. National Parks Service, Sheraton Four Points Hotel, Ventura, CA.
- Coonan, T.J., 2011. Thirteenth Annual Meeting: Island Fox Working Group. National Parks Service, Sheraton Four Points Hotel, Ventura, CA.
- Coonan, T.J., 2012. Fourteenth Annual Meeting: Island Fox Working Group. National Parks Service, Sheraton Four Points Hotel, Ventura, CA.
- Coonan, T.J., 2013. Fifteenth Annual Meeting: Island Fox Working Group. National Parks Service, Sheraton Four Points Hotel, Ventura, CA.
- Coonan, T.J., 2014. Sixteenth Annual Meeting: Island Fox Working Group. National Parks Service, Sheraton Four Points Hotel, Ventura, CA.
- Coonan, T.J., Dennis, M., 2006. Island Fox Captive Breeding Program: 2005 Annual Report. National Parks Service: Channel Islands National Park, 1901 Spinnaker Drive, Ventura, CA. 06-02.
- Coonan, T.J., Dennis, M., 2007. Island Fox Captive Breeding Program: 2006 Annual Report. National Parks Service: Channel Islands National Park, 1901 Spinnaker Drive, Ventura, CA. 07-04.
- Coonan, T., Rutz, K., 2001. Island Fox Captive Breeding Program: 2001 Annual Report. National Parks Service: Channel Islands National Park, 1901 Spinnaker Drive, Ventura, CA. 02-01.
- Coonan, T.J., Schwemm, C.A., Garcelon, D.K., 2010. Decline and Recovery of the Island Fox: A Case Study for Population Recovery. Cambridge University Press.
- Edelstein-Keshet, L., 2005. *Mathematical Models in Biology*. Society for Industrial and Applied Mathematics, Philadelphia, PA, USA, ISBN: 0898715547.
- ESRI, 2011. ArcGIS Desktop (Version 10.3). <http://www.esri.com/software/arcgis>.
- Gaff, H., 2011. Preliminary analysis of an agent-based model for a tick-borne disease. *Math. Biosci. Eng.* 8, 463–473.
- Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010. The ODD protocol: a review and first update. *Ecol. Model.* 221, 2760–2768.

- Heppenstall, A., Crooks, A., See, L., Batty, M., 2012. Agent-Based Models of Geographical Systems, first ed. Springer, Netherlands.
- Hoppensteadt, F., 2006. Predator-prey model. Scholarpedia 1 (10), 1563.
- Hosking, J.R.M., Wallis, J.R., Wood, E.F., 1985. Estimation of the generalized extreme-value distribution by the method of probability-weighted moments. Technometrics 27 (3), 251–261. <https://doi.org/10.1080/00401706.1985.10488049>.
- Kot, M., 2001. Elements of Mathematical Ecology. Cambridge University Press. <https://doi.org/10.1017/CBO9780511608520>.
- Latta, B.C., 2004. Channel Islands Golden Eagle Translocation Program Summary Report. The Nature Conservancy.
- Moore, C.M., Collins, P.W., 1995. *Urocyon littoralis*. Mamm. Species 489, 1–7.
- QGIS Development Team, 2009. QGIS Geographic Information System (Version 3.0). <https://qgis.org>.
- Railsback, S.F., Grimm, V., 2005. Individual-Based Modeling and Ecology. Princeton Series in Theoretical and Computational Biology, Princeton University Press, Princeton, NJ.
- Railsback, S.F., Grimm, V., 2011. Agent-Based and Individual-Based Modeling: A Practical Introduction. Princeton University Press.
- Roemer, G.W., Smith, D.A., Garcelon, D.K., Wayne, R.K., 2001. The behavioural ecology of the island fox (*Urocyon littoralis*). J. Zool. 255 (1), 1–14. ISSN 1469-7998. <https://doi.org/10.1017/S0952836901001066>.
- Roemer, G.W., Donlan, C.J., Courchamp, F., 2002. Golden eagles, feral pigs, and insular carnivores: how exotic species turn native predators into prey. Proc. Natl. Acad. Sci. 99 (2), 791–796.
- Sanchez, J., Hudgens, B., 2011. Spatial Ecology of the Island Fox. Department of Defense Legacy Resource Management Program.
- Schwemm, C.A., 2008. Tenth Annual Meeting: Island Fox Working Group. National Parks Service, Sheraton Four Points Hotel, Ventura, CA.
- Scott, S.M., Bodine, E.N., Yust, A., 2014. An agent-based model of Santa Cruz island foxes (*Urocyon littoralis santacruzae*) which exhibits an Allee effect. Lett. Biomath. 1 (1), 97–109.
- Todd, C.S., 2000. Golden Eagle Assessment. Maine Department of Inland Fisheries and Wildlife.
- Vissman, S., 2004. Island Fox: Management Guidelines for Species at Risk on Department of Defense Installations. NatureServe.
- Weisstein, E. W., n.a.-a. Albers Equal-Area Conic Projection. From MathWorld-A Web Resource, <http://mathworld.wolfram.com/AlbersEqual-AreaConicProjection.html>.
- Weisstein, E. W., n.a.-b. Lambert Conformal Conic Projection. From MathWorld-A Web Resource, <http://mathworld.wolfram.com/LambertConformalConicProjection.html>.
- Wilensky, U., 1999. Netlogo. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL.
- Research, Wolfram, 2010. Mathematica 8.0.