Where's the Scrub? Aye, There's the Rub

Victoria L. Chiou
Andrew Carroll
Jessamyn J. Liu
Maggie L. Walker Governor's School
for Government and International Studies
Richmond, VA

Advisor: John A. Barnes

Abstract

We use data from eight patches inhabited by scrub lizards in logistic regressions to predict from the area of sandy habitat the average fecundity, juvenile and adult survivorship, and total population of a patch.

From the viewpoint of evolutionary biology, we analyze the marginal benefit and risk for an individual lizard migrating. The probability of dying during migration is 30%, with a 0.3% marginal risk per meter migrated.

We determine which patches at Avon Park Air Force Base are self-sustaining and which are sustained by migration; our model is 76% accurate in predicting whether a patch is occupied.

We recommend removing encroaching vegetation through roller-cutting as opposed to controlled burning, due to the high intensity of a fire required to burn scrub and due to the public discomfort with controlled burning.

Introduction

Because of the immense diversity within the Florida sand pine scrub ecosystem, the World Wildlife Organization has granted the Florida scrub "ecoregion" status; at a mere 3900 km^2, it is among the smallest ecoregions of the contiguous United States.

This ecoregion is a "naturally fragmented archipelago of habitat islands" [Branch et al. 1999]. Isolated light-colored patches of sandy soil, obscured by litter and lichens, are surrounded by areas of dense scrub thicket.

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The Florida scrub is rapidly deteriorating due to human development and replacement of scrub by citrus groves, pasturelands, and pine plantations. Extensive human disturbance and development of scrub areas has increased the fragmentation and isolation of scrub patches, and led to fire suppression.

Florida scrub must be maintained by periodic intense fires. Scrub patches burn naturally every 15 to 100 years [Harper and MacAllister 1998]. Because of human development, fires have been suppressed for the past 80 years; this suppression has led to a decrease in the number of available scrub patches, reduction of scrub patch size, decline of habitat quality, and increased patch isolation [Branch et al. 1999].

Conservation efforts have involved proposals for prescribed burning and buying up scrub lands for consolidation. Scientists and conservationists should combine their efforts to provide the public with critical information on the needs of imperiled, threatened, and endangered species, particularly those endemic to the Florida scrub area. While much government money has been directed towards wetland conservation, the Florida scrub contains more vulnerable species than the wetlands for which the state is known [Harper and MacAllister 1998]. If appropriate measures are not taken to protect habitat, the imperiled Florida scrub lizard will become endangered or even extinct. Before further policies on prescribed burning or mechanical methods of vegetation clearance can be implemented, the public must understand the benefits of such policies.

Food for the Brood: Lizard Fecundity and Survivorship

Assumptions

- The only factors that contribute to change in population are fecundity and survivorship.

- There are numerous definitions and levels of fecundity. We use *annual female fecundity*, the total number of offspring per female in one full year.

- We do not consider age a determinant of sexual maturity, except that lizards do not reproduce in the same season in which they were born, regardless of size [Antonio 2000].

Fecundity is affected by the size and age of the lizard, available food and nutrition sources, sex ratio, environmental fluctuations, temperature, and humidity of the area. Sex ratios of lizard populations are typically about one-to-one.

Clutches range from two to eight eggs per clutch [Branch and Hokit 2000]. The major factor affecting clutch size is the size of the lizard, which is proportional to snout-to-vent length (SVL), according to the function

$$y = 0.21(\text{SVL}) - 7.5. \qquad \textbf{(1)}$$

Body size is critical because lizards require stored energy (in the form of fat reserves) to produce eggs; body size increases with age.

Lizards lay from three to five clutches in one reproductive season; this number is the *clutch frequency*. Since direct data collection is nearly impossible, clutch frequency is often estimated as the duration of the active season divided by the time to produce a clutch. This estimate may be inaccurate due to variability in the time to produce a clutch and the reproductive season being shorter than the active season.

The incubation time is 30 days; so with a reproductive season of late March through June, clutch frequency is approximately three. This agrees with researchers who determined that there are not enough data to calculate clutch size or clutch frequency and who thus assumed an average of four eggs per clutch and three clutches per season [Branch et al. 1999].

Survivorship is the ratio of lizards surviving at age x over those who were living at age $(x-1)$; it is generally measured by sequential sampling of a marked cohort of individuals. Losses due to emigration are small compared to those from mortality and tend to be balanced by gains from immigration.

Using **Table 1** of the problem statement and applying **(1)** with the assumptions of three clutches per season of four eggs each, we find:

- $F_a = 5.33$, average annual fecundity;
- $S_j = 0.185$, the juvenile survivorship rate from age 0 to 1 (between birth and the first reproductive season); and
- $S_a = 0.106$, the average survivorship rate.

Modeling Female Lizard Growth

Female reptile growth can be split into three periods:

- growth until sexual maturity (period 1),
- growth after sexual maturity until optimal size (period 2), and
- growth after optimal size (period 3).

Growth is generally rapid until reaching sexual maturity and much slower thereafter [Heatwole 1976].

The growth rate in period 1 may be estimated from the average hatchling size, lizard size at sexual maturity, and time necessary to reach maturity. The lizard is is 21 mm at hatching but reaches 45 mm by sexual maturity in 10 to 11 months [Gans and Pough 1982; Branch et al. 1999]; hence the growth rate is 2.2 to 2.4 mm/month.

After sexual maturity, the lizard continues to grow at a lower rate to optimal size. If the lizard is still alive after this point, its rate tapers to a growth rate that continues for the rest of its life. Since most scrub lizards do not live past two years of age [Branch et al. 1999], we assume that the growth between ages 1 and 2 years in **Table 1** of the problem statement is period-2 growth (0.83 mm / month, on average), and the growth between 2 and 3 years of age is period-3 growth (0.02 mm / month, on average).

Scrub, Sand, and Survivorship: Modeling Lizard Carrying Capacity, Fecundity, and Survivorship

Much of the variation in annual female fecundity, juvenile survivorship, adult survivorship, and density is explained by patch size and amount of sandy habitat. However, 97% of the variation in sandy habitat area is explained by the size of the patch; so in our regression analyses, we use only one of those two variables (whichever one has higher correlation with the variable of interest).

The area of the sandy habitat has a large impact on average fecundity ($r^2 = .77$), with predicted fecundity varying from 5.9 to 11.7 from the smallest to the largest patches. Area of sandy habitat also greatly affects ($r^2 = .81$) adult survival rate, with predicted values ranging from .07 to .16.

However, survivorship of juvenile lizards is less related to patch size ($r^2 = .66$), varying from .14 to .20. For juveniles, the probability of successful emigration may play a significant role in survivorship.

Juvenile survivorship and adult survivorship are closely linked ($r^2 = .96$). This is expected, since juveniles are not so different in structure and metabolism from adults in predators, habitat, or food sources.

The *proportion* of the patch occupied by sandy habitat is an extremely poor predictor of average fecundity, survivorship, or density, with the highest r^2 being .04.

We use a logistic model to predict average fecundity, juvenile survivorship, and adult survivorship from the area of sandy habitat. We choose a logistic model because as the area of sandy habitat increases, fecundity and survivorship do not continue to increase without bound, as would occur with a linear model, but instead tend toward a maximum.

The regression reveals the following relationships with area covered by sandy habitat (x):

$$\begin{aligned} \text{annual fecundity} &= 10.3\bigl(1 + 1.42e^{-0.096x}\bigr) \\ \text{juvenile survivorship} &= 0.179\bigl(1 + 0.89e^{-0.169x}\bigr) \\ \text{adult survivorship} &= 0.139\bigl(1 + 1.93e^{-0.123x}\bigr). \end{aligned} \tag{2}$$

To model carrying capacity, we calculated the number of lizards in each patch by multiplying density by patch size, using the data in **Table 1** of the problem statement. We regressed population density on patch size z ($r^2 = .87$)

and predicted number of lizards in a patch as population density predicted times size of the sandy patch, arriving at:

$$\text{number of lizards} = 0.227z^2 + 51.2z, \tag{3}$$

with $r^2 = .999$. Does this equation also give a good estimate for the carrying capacity of a patch? Lizard populations tend to be quite stable, fluctuating only mildly from carrying capacity [Gans and Tinkle 1977]. That the actual lizard populations correspond so closely to the predicted values suggests that the populations are at carrying capacity.

Lizard Migration Motivation

It is difficult to determine the probability of a lizard dying during migration based on the proportion of lizards recaptured at various distances from location of initial capture. That the proportion recaptured decreases with increasing distance could be the result of lizards dying between each of the recapture sites or of lizards ceasing to migrate after having traveled a certain distance.

We could use the average speed of dispersal (2.5 m/day) to derive the mortality rate for each day migrated [Branch et al. 1999]. However, doing so assumes that no lizard reach its destination: All are killed en route to an ideal location that is theoretically an infinite distance away. To calculate accurately the probability of dying during migration, we need to analyze the cause of migration.

There are no conclusive data why lizards migrate. Other animals migrate based on the availability of food, space, shelter, or reproductive partners, but apparently a universal 10% of juvenile scrub lizards migrate regardless of any environmental attribute so far measured.

An individual's movement to a new patch brings genetic material. Can this influx of genes be shown to benefit the lizard population and the individual lizard?

For any species to survive, it must use a reproductive strategy that allows rapid adaptation relative to changes in the environment. Less-evolved species rely heavily on genetic diversity, natural selection, and learned behavior to maintain adaptability, as well as on producing far more offspring in a short span of time than can survive. As a result, the population of lizards in a patch exhibits little genetic diversity.

The individual lizard must derive a benefit from having the only offspring in a patch with a genetic advantage, or evolution would not select for lizards that emigrate at a rate of 10%. The potential benefits of migration are moving to an area with

- greater fecundity,
- greater survivorship, or
- an advantage for progeny over other lizards.

The potential risks are

- moving to an area with with lesser fecundity,
- moving to an area with lesser survivorship, and
- dying en route.

Due to the strong correlation (90%) between area of sandy habitat and number of lizards in a patch, most lizards live in patches with fecundity and survivorship rates above those of the average patch. Thus, the only advantage of emigrating introducing genes with a selective advantage in the new patch.

By moving to a different patch, the predicted number of offspring falls from 10.1, the average fecundity of all lizards, to 7.8, the average fecundity of all patches. (We assume that males have the same fecundity rate as females.) The decrease of 2.3 indicates a penalty of producing 23% fewer offspring by migrating.

For 10% of juveniles emigrating, the net benefit of successful emigration should theoretically be 10% as well. The average distance traveled by migrating lizards was 105.5 m, so the marginal benefit to traveling 1 m successfully should be 100% / 105.5 m = .095% / m.

Beyond 400 m, no lizards are captured. We assert this as the distance beyond which no lizards emigrate; at this distance, the net benefit of migration is -100%.

Since the migration penalty in fecundity does not vary with distance traveled, we can relate marginal benefit per meter to the average probability of dying en route:

$$b = 0.0948d - rd - 22.8,$$

where

d = distance traveled (m),

b = the net benefit of migration (%),

r = the marginal risk per meter of dying en route, and

22.8 is the percentage fecundity penalty of migrating to an average patch.

At a distance of 400 m, the net benefit is -100%. We put $d = 400$, $b = -100$, and solve for r, finding $r = 0.288\%$ deaths / meter.

We estimate the average death rate D for all emigration based on the average distance traveled (105.5 m). Thus, the average death rate for emigration is $D = 0.288\%/\text{m} \times 105.5\ \text{m} = 30.4\%$. The average mortality rate for the juvenile population due to migration equals D (30.4%) times the propensity to migrate (10%), or 3%.

Patch Occupation and Viable Population

Previous lizard studies at Avon Park Air Force Base use a measure of isolation S_i of a patch i:

$$S_i = \sum p_j e^{-d_{ij}} A_j,$$

with the sum taken over all patches j with $j \neq i$ [Branch et al. 1999]. Thus, isolation is a function of

- d_{ij}, the distance between patches i and j; and
- A_j, the area of patch j.

The value of p_j is 1 if patch j is occupied, 0 otherwise.

The distance between patches determines the difficulty of movement between patches, while the area of the patch determines the possible number of migrants, since area has a strong correlation with patch population.

Branch et al. [1999] determine that the probability that a patch is occupied is given by

$$P_i = \frac{\exp(0.61A_i + 0.05S_i - 5.22)}{1 + \exp(0.61A_i + 0.05S_i - 5.22)},$$

where for patch i we have

P_i = probability that the patch is occupied,

A_i = area of the sandy habitat of the patch, and

S_i = the isolation parameter for the patch.

This equation predicted patch occupancy for scrub patches within the Avon Park Air Force Range with 89% accuracy [Branch et al. 1999]. However, this equation can be used only if it is known which patches are occupied; yet the goal is to predict patch occupation without knowing which patches are occupied.

To accomplish this latter goal, we use our logistic regressions **(2)**. We formulate the ability of each patch to sustain its population by comparing average fecundity to the average number of deaths through the equation:

$$\text{Sustainability} = 1 + \left(F_a - \left[\frac{1}{S_j} + \frac{1}{S_j S_a} + \frac{1}{S_j S_a S_a} + \cdots + \frac{1}{S_j S_a^n} \right] \right).$$

This equation gives the sustainability of a patch: the average number of lizards that a single lizard will yield each year from the patch. The number of lizards in the patch will grow, stay the same, or decrease, depending on whether sustainability is below 1, equal to 1, or above 1.

According to our logistic regressions, only patches 2, 9, 12, 15, and 17 have sustainability greater than 1. They are thus the only patches capable of maintaining a population, apart from migration.

Migration

To factor in the effects of migration, we use a long-term approach. We assume that each patch is at carrying capacity, so excess lizards that are produced in patches with sustainability greater than 1 migrate to other patches. For each patch, we estimate the number of lizards each year generated above replacement level by multiplying the predicted population by the sustainability, using **(3)**.

We assume that lizards migrate patches to other populated patches uniformly; if an inhabited patch is adjacent to two uninhabited patches, half of the migrating lizards in the inhabited patch attempt to migrate to one inhabited patch and the other half attempt to migrate to the other patch. We calculate the number of lizards that die between patches using the previously calculated average death rate for emigration, $r = 0.288\%$.

We apply these formulas in a series of "rounds" that move the number of offspring above the equilibrium number from the inhabited patches to the uninhabited ones. In each "round," the effect of migration is first calculated between adjacent inhabited patches, then the effect of migration to uninhabited patches is taken into account.

After each round, patches at equilibrium are classified as inhabited. Patches that changed from a yearly deficit of lizard production to a yearly surplus, due to migration, are placed into the next round as occupied patches that generate migration into unoccupied adjacent patches. After six rounds, all the patches are either at equilibrium or have a yearly deficit of lizards even with migration.

Our model predicts that patches 2, 3, 9, 10, 11, 12, 15, 17, 21, 22, and 23 are occupied. This accurately predicts the occupancy status of 22 of the 29 patches (76%). Furthermore, the model is not systematically biased: four unoccupied patches (2, 3, 9, and 10) are predicted as occupied, and four occupied patches (5, 13, and 23) are predicted as unoccupied.

Assuming that the population in an inhabited patch is assumed at carrying capacity, the total number of lizards in the Range is 17,679.

A Policy for Controlled Burning

Florida scrub must be maintained by periodic intense fires: Flora and fauna of the scrub require fire to disperse seeds, regenerate, and clear dense brush. As vegetation becomes increasingly dense, sandy patches experience fragmentation and may disappear [Harper and MacAllister 1998]. Natural burns occur every 15 to 100 years. The U.S. Army Corps of Engineers recommend prescribed fires every 8 to 20 years [Harper and MacAllister 1998].

Prescribed fires are a heatedly debated remedy, particularly since scrub lands have a high real-estate value. Nearby homeowners fear that prescribed fires may get out of control, as happened with recent ones in Texas and California that destroyed more than 200 homes.

Part 1: Vegetation Model

Assumptions

- The 6% increase in vegetation density per year noted in the problem statement decreases sandy habitat and applies to scrub areas in their entirety and to all Florida scrub areas.
- The rate of increase of vegetation density remains constant for subsequent years.

We use a spreadsheet to simulate overgrowth of vegetation. Using **Table 3** of the problem statement, we calculate the percentage of sandy habitat per patch; the average is 39.2%. Per our assumption, we apply this average to the whole Florida scrub ecoregion.

Initial sandy habitat area, or sandy habitat area directly prior to the establishment of the 6% vegetation density growth rate, is represented by

$$S_o = 390{,}000(0.392) = 152773.$$

Amount of remaining sandy habitat in subsequent years, given a 6% vegetation density growth rate, is calculated from

$$S_t = 1 - .06S_{t-1},$$

whose solution is

$$S(t) = 152{,}773e^{-0.0619t}$$

for time t in years.

Assessing the Model

Our model relies strongly on statistical analyses of experimental data and evolutionary theory to create equations and theories to apply to all scrub lizard populations. This is necessary because of the scarcity of documented and quantified relationships between vital attributes of scrub lizards (such as food, shelter, and space requirements, predatory and density limitations, the influence of temperature and rainfall, or why scrub lizards migrate) and scrub lizard fecundity and survivorship. As a result, our model goes a long way with few concrete data, predicting such diverse attributes as marginal risk of dying per meter migrated and the number of years that the population of a patch can survive without encroaching vegetation being cleared.

Because we use few constants in our equations and rely more upon logistic relationships between data and basic evolutionary principles, our model should be easily adaptable to most species that live in patches. Only a few data about fecundity, survivorship, relationship to habitat, population density, and tendency to migrate are required to predict which patches are be inhabited, which patches are necessary to sustaining a population throughout the region, the net benefit of migrating, and the relationship between size and fecundity. Although our model analyzes the population dynamics of the scrub lizard, it could just as easily apply to the scrub jay.

Another advantage of our model is the speed and ease with which it can be run and adapted. Our model requires only a spreadsheet program, a calculator that can perform logistic regressions, and minimal data-entry time.

Although it would have been possible to relate patch size, sandy habitat area, fecundity, survivorship, and density with a multiple regression, we believe that a logistic regression better represents the diminishing returns of increases in patch size and sandy habitat on survivorship and fecundity.

A weakness of this approach is that our model is not very robust. Because there are so few data, our assumptions are flawed, and so the only accurate piece of our model is the logistic equations, which are not useful for predicting which patches are inhabited. However, all our assumptions are grounded in basic principles of biology and evolution. Also, our model is at greater risk than most if the data are inaccurate, because it relies on so few data points.

Our Proposal

The risks and opposition of controlled burning outweigh support of conservationists. There is a tremendous risk to human life and property incurred by controlled burning, such as the voluminous amounts of noxious smoke that would prove detrimental to air quality and population health [Harper and MacAllister, 1998]. Inappropriate smoke management would result in severe visibility reduction for vehicle operators, and pose a health risk to those with respiratory problems.

Alternatives include numerous upland management strategies, such as scraping, chaining, cabling, railing, rollerchopping, shredding, and rotobeating. The U.S. Army Corps of Engineers have found that many scrub flora species respond nearly equally to fire and mechanical methods. Other studies indicate that mechanical methods stimulate seed germination of some scrub species [Harper and MacAllister 1998].

We recommend that mechanical methods such as rollerchopping be implemented in place of controlled burning. Rollerchopping involves a tractor or bulldozer pulling steamroller drum with chopper blades through the brush [Payne and Bryant 1994]. Rollerchopping has resulted in reduction of coarse woody debris, increased open sandy habitat, increased stand quality—and higher lizard density.

Consolidation of scrub patches would likely have a positive effect on lizard populations [Branch et al. 1999]. The U.S. Army Corps of Engineers recommends creation of larger scrub patches [Harper and MacAllister 1998], which can be achieved through restoration of surrounding degraded scrub patches. Sand roads should be used to connect patches, to facilitate migration, to improve gene flow, and to recolonize of patches [Harper and MacAllister 1998]. Disturbances such as road creation and extensive development should be avoided. Roads and construction act as barriers that increase the fragmentation of existing scrub patches.

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