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A Spatially Explicit Model of Red Imported Fire Ant Behavior for Managing Species at Risk on Military Lands

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Abstract: Cave cricket populations are essential to the survival of many rare invertebrates that are endemic to the karst regions of Fort Hood, TX. These crickets bring organic matter into the caves, where it serves as an energy source for a variety of karst invertebrates. At Fort Hood, Red Imported Fire Ants (RIFA) migrating from South America into the southern United States prey upon cave crickets, which potentially threatens some populations of rare invertebrates. Observational studies have documented this risk, and Fort Hood wildlife biologists are actively managing fire ant mounds located near caves in order to protect karst invertebrates.

This report outlines a method for developing a simple, localized computer model that can be used as a cost-effective tool in proactive cave management activities. The model developed in this study combines the expertise of natural resources personnel, information from field studies, and digital mapping data to create a spatially explicit model of RIFA behavior as relates to cricket populations. The model was developed using the public domain NetLogo modeling program and did not require the intervention of a computer programmer. Ecologists and biologists need no computer expertise to develop NetLogo models, and the results are transparent enough to be understood by other technical peers with no computer expertise.

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Preface

This study was performed for Headquarters, U.S. Army Corps of Engineers (HQUSACE), under Research, Development, Test, and Evaluation (RDTE) Program 62272089600, “Base Facility Environmental Quality”; project 140644, “Habitat-Centric SAR (Species at Risk) Research – Multi-Species PVA (Population Viability Analysis.” The technical monitor was Dr. William D. Severinghaus, CEERD-CV-T.

The work was performed by the Ecological Processes Branch (CN-N) of the Installations Division (CN), U.S. Army Engineer Research and Development Center – Construction Engineering Research Laboratory (ERDC-CERL). At the time of publication, Dr. Alan B. Anderson was Chief, CEERD-CN-N; Dr. John T. Bandy was Chief, CEERD-CN; and Dr. Severinghaus was the Technical Director for Military Ranges and Lands. The Deputy Director of ERDC-CERL was Dr. Kirankumar Topudurti and the Director was Dr. Ilker Adiguzel.

The authors would like to especially thank Dr. Steven Taylor of the Illinois Natural History Survey, who provided valuable guidance to this effort; and to Mr. Charles Pekins, Wildlife Biologist at Fort Hood, TX, who provided excellent review comments on an early draft of this report. Also, Gordon L. Cohen, CEERD-IS-L, is acknowledged for his editing, rewriting, and related persistent efforts as required to complete this report.

COL Gary E. Johnston was the Commander and Executive Director of ERDC, and Dr. James R. Houston was the Director.

Unit Conversion Factors

Multiply	By	To Obtain
acres	4,046.873	square meters
degrees Fahrenheit	$(F-32)/1.8$	degrees Celsius
miles (U.S. statute)	1,609.347	meters
yards	0.9144	meters

1 Introduction

1.1 Background

Fort Hood, Texas, is home to rare endemic cave invertebrate species. Although these species are not listed under the Endangered Species Act (U.S. Forestry and Wildlife Service 1994, 2000), they are being carefully studied and managed to avoid listing. The at-risk invertebrates at Fort Hood are found in caves that extend across the entirety of the karst landscape, although many caves are concentrated in remote areas that are not often accessed by people.

The caves beneath Fort Hood lack primary producers and roosting bat populations, a large source of energy input in other cave systems. Therefore, the endangered karst invertebrates rely on organic matter vectored into the caves by crickets (*Ceuthophilus secretus*) (Taylor et al. 2003a).

Cricket guano, eggs, and juvenile nymphs are consumed by a number of gastropods (e.g., *Helicodiscus* spp. and *Mesodon* spp.), carabid beetles (*Rhadine reyesi*), and spiders (*Cicurina* spp.), respectively (Taylor et al. 2003). Thus, cave crickets are a keystone resource supplier for the endemic karst communities.

These cave crickets also allow for a relatively easy method of measuring cave health, without a negative impact on the species of interest. While the endangered species are hard to find, due to their relative lack of numbers and living deep within caves, *Ceuthophilus secretus* is populous and leaves the cave each night to forage.

However, the cave crickets are now at risk from an exotic species that has invaded Fort Hood. The Red Imported Fire Ant (*Solenopsis invicta*), originated from South America, and first appeared in the United States in the 1930s (Taber 2000).

The Red Imported Fire Ants (RIFA) spread quickly, and successfully invaded numerous southern states. Among these are established colonies in Texas (Cokendolpher and Phillips 1989) that have been found within 15 m of caves in Fort Hood (Elliot 1992).

RIFA are aggressive omnivores that have been known to eat millipedes, salamanders, earthworms, and both live and dead cave crickets (Elliot 1992; Wojcik et al. 2001). This makes them a broad spectrum pest to the management of any endangered invertebrate species within their territory. A number of observational studies have documented the potential for detrimental impacts of RIFA on the karst community. Taylor et al. (2003b) documented widespread colonization of Fort Hood by RIFA, including those areas with caves.

Both cave crickets and RIFA are opportunistic omnivores that eat nearly everything except raw plant materials (Campbell 1997; Elliot 1992; Taber 2000; Cokendolpher et al. 2001). Thus, interspecific competition for resources is likely. In addition, RIFA foraging of cricket eggs and nymphs has been observed inside caves on Fort Hood (Reddell 2001; Taylor et al. 2003a), especially in summer months when high temperatures drive RIFA deep into the soil. Elliott (1992) has observed RIFA preying upon live adult crickets, along with many other cave invertebrates.

These field studies have motivated the management of fire ant mounds in the vicinity of caves, in order to protect karst invertebrates. However, no model to date has investigated the broader impacts of a different management strategy as it affects cricket populations and, ultimately, the sustainability of karst communities and fire ant abundances on a landscape scale. The U.S. Army Engineer Research and Development Center – Construction Engineering Research Laboratory (ERDC-CERL) has developed an expedient simulation model that provides the ability to track RIFA agents in the form of mounds across a spatial and temporal landscape, and to assess the impact of the invasive species on the native community.

1.2 Objectives

The objectives of this model are to incorporate the information from field studies into a spatially explicit model of fire ant and cricket behavior, and to document the effectiveness of RIFA management in order to ensure the long-term sustainability of karst communities. The results will aid in identifying the level of management needed for caves of varying size, as well as direct areas of future research.

A general objective of this work was to demonstrate how biologists and Army installation land managers may quickly develop a simple computer-based model, using location-specific data and parameters with public-

domain software, that can rapidly simulate the impacts of alternate habitat-management strategies. The intent is to illustrate that simple, expedient models may be developed by personnel who have no expertise in model building, and how those models may add considerable value to land management activities.

1.3 Approach

The model described here was developed using NetLogo 4.0.2, a software tool developed at the Center for Connected Learning of Northwestern University, <http://ccl.northwestern.edu/netlogo/>. Details of the development methodology are described in Chapter 2.

1.4 Scope

The RIFA model demonstrates an expedient method that biologists and land managers can use to build simple data-driven models that can test the impacts of different installation land-management decisions. This method enables technical subject-matter experts to develop a spatially explicit localized model without having any previous simulation modeling experience. The model documented here was developed for a specific application, as described in the text. However, it can be extended, altered, or recreated by users with an interest in different sets of species, data, or parameters that are relevant to other locations. For example, the basic model could be modified to include species migration activity, population distribution regions, and microclimate impacts.

1.5 Mode of technology transfer

The RIFA model is being presented at seminars and conferences to inform military installation land managers of (1) available capabilities for rapidly constructing useful models of ecological and environmental processes, and (2) the availability of the RIFA model for direct application or adaptation to the environment at a specific locale. The RIFA model is available to the public as a free download at <http://earth.cecer.army.mil/>.

2 Model Development

2.1 Model description

Interactions between RIFA, cave crickets, and resources in the environment are modeled using NetLogo 4.0.2 software. RIFA and crickets are modeled as colonies, labeled “Mound” or “Cave,” respectively. Both obtain resources from the environment, but only mound colonies reproduce.

Resources obtained from the environment directly influence the number of individuals contained within the mound or cave. One of the primary goals of this model is to realize the potential impact of RIFA foraging and raiding on native karst fauna (cave crickets), particularly if fire ant populations continue to grow at rates consistent with the last 50 years.

An overview of interactions within the model is displayed in Figure 1.

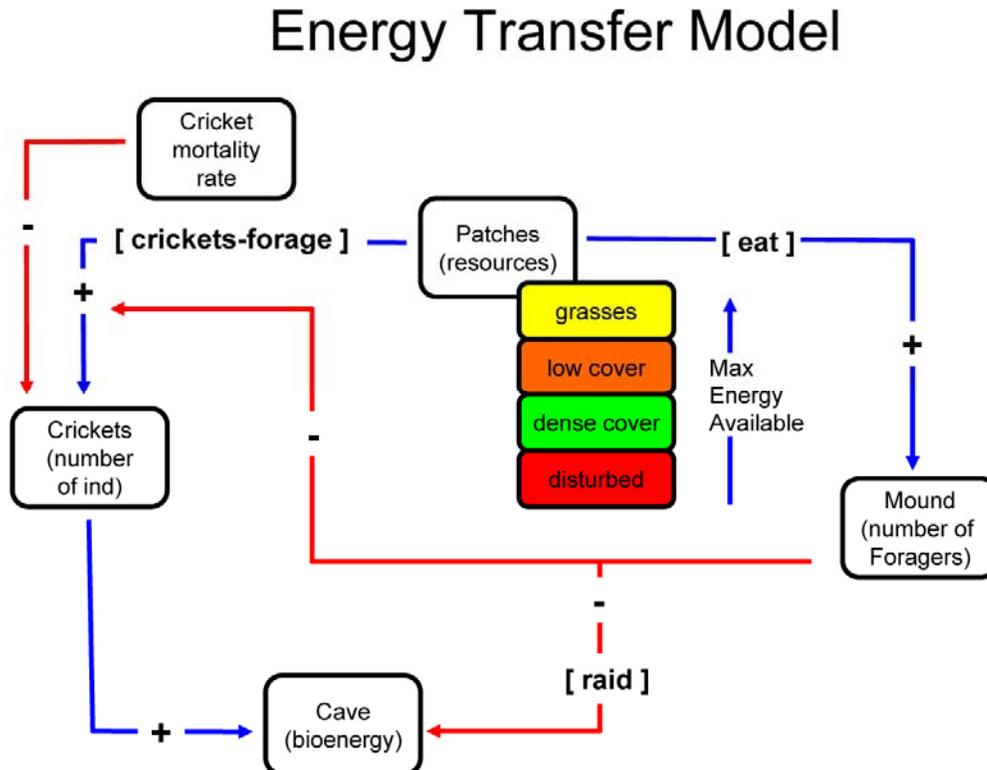


Figure 1. Overview of interactions within model.

Other goals of the model are the assessment of RIFA management and evaluating potential parameters of interest for future research. Spot mound eradication using hot water is a common management technique, and will be tested in the model for a period of ten years. The model will also assess various parameters (cave-carrying capacity, intrinsic rate of growth, cave raiding by RIFA) to understand which parameters cause significant deviance in cave viability, both with and without management. This will focus further studies in data acquisition for cave managers, and provide a framework for cost-effectiveness of future RIFA management.

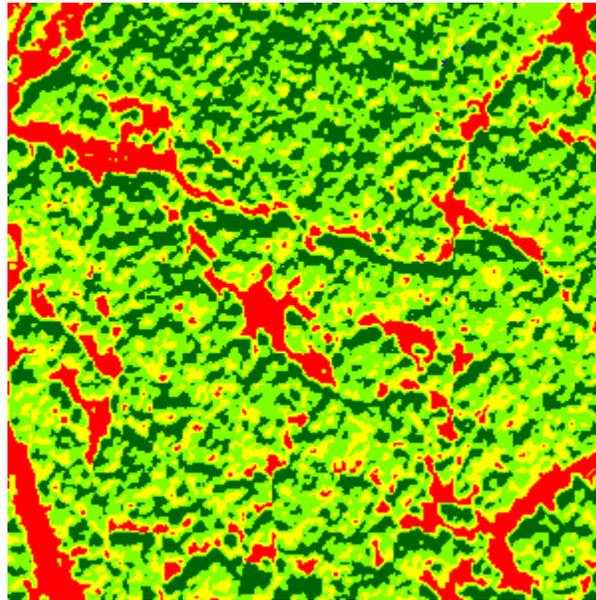
2.2 World details

Satellite map images were downloaded from U.S. Geological Survey (USGS) Seamless Server (<http://seamless.usgs.gov>), and coded with NLCD 2001 Land Cover Data.

ERDAS IMAGINE (<http://www.erdas.com/>) was used to convert each pixel into one of four colors, each matched to a specific type of land cover. Upon importing the image into the NetLogo model, the colors were changed for ease of reference into the following:

- RED = disturbed area (examples: dirt roads and land development)
- YELLOW = grassland
- BROWN = low density cover (examples: shrubs and small trees)
- LIME = high density cover (examples: high density trees)

Each pixel coded represents a 10 m x 10 m plot of land. The finished world view can be seen in Figure 2. Within the model's world, there are intermittent areas of high and low cover, along with diagonal streaks of disturbance that may have resulted from vehicle movement, the collapse of trees, or human activity. In the lower left corner of the model's world is a streak of disturbance. This is the starting point for the introduction of mounds. From here, three mounds are introduced and will propagate across the landscape test location, as detailed below.



RED = disturbed area (e.g., dirt roads, land development);
YELLOW = grassland; BROWN = low density cover (e.g., shrubs and small trees);
LIME = high density cover (e.g., high density trees).

Figure 2. World view of NetLogo model area shown as imported and coded LCID image.

2.3 Resources

Each imported pixel is represented in NetLogo by a “patch,” and assigned a maximum-energy variable, based on the specific land type. To simulate replenishment of resources from influx of prey species, growth of edible plant matter, etc., the available energy of each patch has a 20% chance of increasing during each week, up to its maximum-energy variable. This prevents the caves and mounds from depleting their resources and dying off, and creates a more realistic setting of use and growth of resources. Caves and mounds will attain a stable carrying capacity based on the local resources available, and the resource replenishment within their respective foraging range.

3 Description of Crickets Model

3.1 Cave stabilization

Within the model, the caves are given a period of time without competing with mounds, or being preyed upon by mounds. This is to allow for each cave to reach a stable population size comparable to that found in the wild. It takes approximately 5 – 10 years for the cricket population to stabilize, without any fire ants present. (The model allows for 10 years to pass before the introduction of mounds.)

3.2 Foraging range

Caves rely on foraging crickets to bring in bioenergy. The minimum and maximum range for crickets' foraging distance from the cave is 30 m and 100 m, respectively (Taylor et al. 2003a). Caves with larger populations of crickets have a greater range. Below 30 m from the cave, cricket density during foraging is uniform. At greater ranges (up to 100 m), the density of crickets drops, ultimately reaching a density of no crickets at 100 m.

Since the movements of individual crickets are not tracked in this model, this function of cricket density allows for the reduction of available energy to the crickets — the further the patch from the cave, the less energy will be gathered, due to lower cricket density. This simulates both the decreased number of crickets at distant ranges from caves as well as the reduced energy consumption at the further ranges, due to more energy being expended while retrieving nutrients farther from the cave.

3.3 Birth and death

Cricket populations were determined using the Verhulst equation, with varying carrying capacity used to simulate the different sizes of caves at Fort Hood. The intrinsic rate of growth was determined to be within the range of closely-related cricket species, and below that of the faster-reproducing RIFA.

The equation also included a sensitivity to the surrounding conditions, where the impact of decreases in available energy could vary. Within the formula used, a lower number indicated a high sensitivity to available resources.

4 Description of RIFA Model

4.1 Mound foraging range

The RIFA mound sub-model's foraging code is virtually identical to the cave sub-model, due to the similar energy flow. For a RIFA mound, a large percentage of the adult ants are foragers, and leave the mound to gather energy. Their success in bringing in energy means the population of the mound increases, reaching a maximum-carrying capacity of 250,000 ants (Markin et al. 1974). Since RIFA are observed to be more aggressive, more cooperative and more numerous in their foraging than crickets, RIFA will usually gain more energy from the same source when mounds and caves simultaneously forage the same patch of resources.

Mounds will also diminish the available resources in a patch during each week before the caves are able to forage. This is also due to the greater aggression of RIFA over the crickets, as areas that have RIFA show a decrease in crickets numbers (Taylor 2003a). It is believed that the presence of RIFA discourages cricket foraging as they attempt to avoid predation. RIFA also forage during both day and night, but are more dependent on temperature than time of the day. By contrast, cave crickets forage only at night.

4.2 Mound propagation

RIFA typically propagate during mean daily temperatures over 69 °F but below 89 °F (Tana 2002), and with high humidity or rain present. By mapping the weekly mean temperatures together with average rainfall and humidity, we can designate propagation seasons for RIFA (spring and fall in this model). The propagation seasons cause the spread of RIFA across the landscape and higher foraging activity, since alate production requires enormous energy. Propagation is a high-risk activity for RIFA; only 2% of new starts typically result in a successful new mound.

Three factors affect the success of mound establishment: (1) new mounds participating in intraspecific mound raids, (2) new mounds having enough energy resources nearby without high competition, and (3) new mounds being more successful in disturbed areas.

To simulate these conditions within the model, new mounds followed three sets of rules: (1) If multiple new mounds are established on the same patch, they will form into one mound, simulating mounds performing raids in which the losing mounds' workers are absorbed by the winning mounds. (2) New mounds will not be able to establish on the same plot as old mounds. (3) New mounds will be more likely to establish on disturbed areas.

4.3 Mound growth

Mounds were grown based on the methods outlined in Section 3.2. Mound population growth rate was found to be comparable to that in other simulated models (Killion and Grant 1993).

4.4 Mound raiding

Caves at Fort Hood are periodically raided by RIFA. This typically occurs in the summer months, when RIFA stay underground to avoid the heat (Taylor 2003a). To simulate this within the model, caves within the foraging range of a mound were given a 20% chance of being raided each week during the summer season.

Also within the model, caves that are raided lose 100 crickets. This number was chosen as a conservative estimate of the raiding that typically occurs close to the entrance of a cave, or the Twilight Zone, though it is possible that additional raiding occurs in remote regions not accessible by humans (Taylor 2003a).

4.5 Mound management

One common method employed to exterminate RIFA is the injection of boiling water deep into the mounds. Within the model, management of mounds simulated a yearly hot water treatment of RIFA mounds within the foraging radius of caves.

When enabled, each year mounds within the foraging radius of a cave would have a 60% chance of being killed. This is because injecting hot water into the mounds has a 60% success rate, which follows observed data (Nature Conservancy 2000), and allows for reduced, though still present, impact on the caves by mounds.

5 Simulation Results

Results were analyzed using the general linear model software from the SAS company (www.sas.com). Because the random effect for caves was not significant, no random effect was fit to the model. The Tukey-Kramer procedure for analyzing unequal pairlike comparisons was used to adjust for multiple comparisons. No outliers were present, and all runs under all parameters were used.

Most main effect and combined effect parameters within the model were statistically significant. This shows that the presence of RIFA significantly impacts cricket populations at all cave levels ($p = 1.000$). The parameters are also useful in understanding that RIFA significantly impacted crickets, whether or not raiding was turned on, as this could possibly be a point of contention (see Ch. 6, p. 18 of this report).

However, when too much data is significant, it runs the risk of being meaningless. We resolved this with two further steps.

The first step was to account for what was not statistically significant. Establishing these parameters allowed us to understand when no change needs to occur in order to protect cricket populations between situations. These parameters also allowed us to check for model reliability, by comparing situations that should not be significantly different.

The second step was to identify select cases of importance, such as complete cave loss, and large patterns that are not illuminated by the statistical analysis.

The following paragraphs outline these steps in detail.

5.1 Step 1

To check for model reliability, we examined the situations where management techniques were applied, both with and without RIFA present. With no RIFA present, management techniques should not cause any change in the average number of crickets. This was confirmed by our results: average number without RIFA, management on = 91.8%; management off = 91.8%; $p = 1.000$.

However, all other conditions with RIFA being present, whether raiding was turned on or off, and whether management was turned on or off, were highly significant from each other ($p < 0.0001$). This is evidence that management techniques within the model were affecting cricket populations through reduction of RIFA, and not an unknown error in the coding.

Within any setting of sensitivity to resources, the caves with a $K = 1,000$ were consistently at a disadvantage to caves with a $K = 5,000 - 10,000$ (Figure 3).

Caves with a $K = 5,000 - 10,000$ did not have statistically significant differences in their average population across all levels of sensitivity ($p = 0.9533, 0.7179, 0.2905, \text{ and } 0.3259$ for sensitivity; $0.1, 0.2, 0.02, \text{ and } 0.05$ for respectivity). However, caves with a $K = 1,000$ crickets saw significantly fewer percentage of those crickets survive, though the general trend followed that of the caves with a higher K value. Sensitivity appears not to affect caves severely when they have a $K = 5,000$ or higher, but caves with a $K = 1,000$ appear to be impacted greatly by sensitivity.

Concerning the overall average number of crickets, caves that had a $K = 1,000$ were significantly different from caves that had $5,000 - 10,000$ crickets ($p < 0.0001$). While caves that had $5,000 - 10,000$ crickets were significantly different from each other ($p = 0.0002$), the averages were close enough (81.4% and 82.4%, respectively) that this significance can be attributed more to the large sample size, than to an effect between caves that needs to be accounted for with management procedures.

At the most robust sensitivity level (0.2), the presence of RIFA does not significantly affect the number of crickets when they are not raiding caves ($p = 0.9205$). Nor is there a significant change from these if the sensitivity is dropped to 0.1, so long as RIFA are no longer present ($p = 1.000$ when compared to sensitivity 0.2 and no RIFA present, and $p = 0.9899$ when compared to sensitivity 0.2 and RIFA present, but not raiding caves).

Raiding caves plays a roll in differentiating the large and small caves. If RIFA are present and raiding, they impact cave populations at all cave sizes ($p = 1.000$), however, there is no difference between how they impact cave sizes when raiding is turned off ($p = 1.000$). Once raiding is turned on, the number of cave crickets significantly drop at all cave sizes ($p < 0.0001$).

Cave sizes have been seen to ameliorate some of the effects of RIFA. Management significantly increases the level of crickets at all cave sizes ($p < 0.0001$). However, in some cases the same result can be seen through an increase in cave size. To elaborate, the average number of crickets in the smallest cave ($k = 1,000$), when management is turned on, is not significantly different than the next largest cave ($k = 5,000$), when the larger cave does not have management ($p = 1.000$).

Management can also be seen to decrease the number of crickets lost in two larger caves. When management is applied, there is no significant difference between caves of $K = 5,000$ or $K = 10,000$ ($p = 0.5286$). Without management, these two cave sizes are significantly different ($p = 0.0004$), though not as much as is normally seen. As their average population sizes are decreased by less than 2% (80.5% and 79%, for the 10,000 and 5,000 K caves, respectively), this can again be attributed to the large number of runs rather than a decrease that warrants concern.

5.2 Step 2

If no RIFA were introduced, caves continued to stay at , or close to, their K value. However, if mounds were introduced, caves showed a decrease in the number of crickets they held. This decrease led to the loss of entire caves in nine separate conditions, as shown in Table 1. Several other conditions showed a severe decrease in cricket population, but those decreases did not result in complete population loss in any of the four caves in each simulation.

Table 1. Conditions leading to loss of all crickets.

Sensitivity	Max Crickets	Raiding	Management	Ants	AveDead	StDevDead
0.02	1000	TRUE	FALSE	TRUE	2.323	0.979
0.05	1000	TRUE	FALSE	TRUE	1.839	1.003
0.2	1000	TRUE	FALSE	TRUE	1.821	0.983
0.1	1000	TRUE	FALSE	TRUE	1.643	1.096
0.02	1000	TRUE	TRUE	TRUE	0.774	0.845
0.2	1000	TRUE	TRUE	TRUE	0.143	0.356
0.02	5000	TRUE	FALSE	TRUE	0.097	0.301
0.1	1000	TRUE	TRUE	TRUE	0.071	0.262
0.05	1000	TRUE	TRUE	TRUE	0.065	0.250

Table 1 is sorted by the average number of caves that lost all crickets. The average numbers of caves (out of four in each simulation) that “died” are

listed, along with the standard deviation for each design. With one exception, each loss happened to a cave with the lowest maximum carrying capacity. The exception had the next-highest carrying capacity, and the maximum level of sensitivity to resources, with ants present and raiding, and no hot water management of the ants. All possible designs that included small caves with raiding ants experienced some cave loss. This result suggests that smaller caves are more at risk to species loss than caves with large carrying capacity, particularly if the ants use the caves directly for resources as opposed to only competing for outside foods. It also shows that a moderate level of management for the ants may not be sufficient to prevent species loss in smaller caves, as management reduced but did not eliminate complete cricket loss from smaller caves.

Of the nine conditions that lost the most caves, eight had a $K = 1,000$ crickets. This accounted for every condition that had a $K = 1,000$ crickets, with ants present, and raiding turned on. Sensitivity and management implementation had an effect on the average number of caves that lost all crickets – with sensitivity effects having priority over management effects. But, all conditions with $K = 1,000$, and ants performing raids, had at least some where there was a total loss of crickets.

Caves showed a marked reduction in losses when management was turned on, from 1.643 to 0.774. This is despite the finding that the condition having the “worst” sensitivity setting did better, while the condition having the “best” sensitivity setting for caves lost over 1.5 caves, on average.

The only condition to experience complete cricket loss, other than the above-mentioned trend of caves with a $K = 1,000$, was a single condition that included a $K = 5,000$. This condition also included the “worst” case scenarios for the caves: high sensitivity, ants present, raiding turned on, and management turned off. However, this condition only lost, on average, 0.097 caves out of four. Likewise, the average number of crickets in caves under this condition was 1,801. Also, no other conditions that included a $K = 5,000$ lost any crickets.

Similarly, no caves with a $K = 10,000$ crickets experienced complete loss of crickets. However, the lowest number of crickets for a cave with a $K = 10,000$, was 4,045. This is a reduction of over half the maximum crickets, though not a reduction that places the cave at a severe risk of cricket loss.

Large reductions are not uncommon for larger caves, though. While the smaller caves were the most likely to have lost all crickets, caves with a $K = 10,000$ made up a significant portion of those caves that had a severe reduction in the percent of crickets remaining at the end of the trials (shown above, in Table 1). Larger cave populations are still highly impacted by RIFA activity, with several populations losing over half of their maximum capacity.

However, these larger caves stabilize at those reduced populations, whereas the smaller caves cannot support such large reductions. While the largest caves lost over half their populations in some cases, none were completely wiped out. Bottlenecking of the population gene pool may be a problem for larger caves, but loss of population is not as much a problem for the largest caves as it is for the smallest caves.

While reduction relative to K is widespread across all levels of K , those with the fewest absolute number of average crickets are the caves with a $K = 1,000$.

Surprisingly, though, the correlation between the average cricket numbers and the number of caves lost is only -0.504 (correlation only for the 35 smallest caves). The average number of crickets is not tightly proportional to the number of caves lost, and there are even several conditions with lower average cricket numbers and no caves lost than some conditions with caves lost (Table 2).

The average number of crickets puts a cave at risk for complete cricket loss, but does not decide it. At 500 or fewer average crickets, there is likely to be a loss of at least one cave. At average cricket populations of 2,000 or fewer, cave loss is still possible, though far less likely.

Table 2. Simulation results sorted by the percent of surviving crickets.

Sensitivity	Max Crickets	PercentMax	Raiding	Management	Ants
0.02	1000	0.186314 52	TRUE	FALSE	TRUE
0.05	1000	0.32076613	TRUE	FALSE	TRUE
0.02	1000	0.33295161	TRUE	TRUE	TRUE
0.02	5000	0.3602129	TRUE	FALSE	TRUE
0.02	10000	0.40452903	TRUE	FALSE	TRUE
0.2	1000	0.41138393	TRUE	FALSE	TRUE
0.02	5000	0.43519516	FALSE	FALSE	TRUE
0.02	10000	0.43715	FALSE	FALSE	TRUE

Sensitivity	Max Crickets	PercentMax	Raiding	Management	Ants
0.02	1000	0.43952419	FALSE	FALSE	TRUE
0.1	1000	0.4429375	TRUE	FALSE	TRUE
0.02	5000	0.44355484	TRUE	TRUE	TRUE
0.02	10000	0.47659435	TRUE	TRUE	TRUE
0.02	1000	0.48024194	FALSE	TRUE	TRUE
0.02	10000	0.48645806	FALSE	TRUE	TRUE
0.02	5000	0.48657097	FALSE	TRUE	TRUE
0.05	1000	0.65820161	TRUE	TRUE	TRUE
0.05	5000	0.66205968	TRUE	FALSE	TRUE
0.05	10000	0.71096129	TRUE	FALSE	TRUE
0.02	1000	0.71609375	FALSE	FALSE	FALSE
0.02	5000	0.71629375	TRUE	FALSE	FALSE
0.02	5000	0.71637188	FALSE	TRUE	FALSE
0.02	1000	0.71645313	TRUE	FALSE	FALSE
0.02	5000	0.7164625	FALSE	FALSE	FALSE
0.02	10000	0.71648047	TRUE	TRUE	FALSE
0.02	10000	0.71656875	FALSE	FALSE	FALSE
0.02	10000	0.71663203	TRUE	FALSE	FALSE
0.02	5000	0.71667188	TRUE	TRUE	FALSE
0.02	10000	0.71667656	FALSE	TRUE	FALSE
0.02	1000	0.716875	FALSE	TRUE	FALSE
0.02	1000	0.71692188	TRUE	TRUE	FALSE
0.05	5000	0.73736452	FALSE	FALSE	TRUE
0.05	10000	0.75688917	FALSE	FALSE	TRUE
0.05	1000	0.75910484	FALSE	FALSE	TRUE
0.05	5000	0.77403065	TRUE	TRUE	TRUE
0.05	10000	0.78235484	TRUE	TRUE	TRUE
0.05	1000	0.79287097	FALSE	TRUE	TRUE
0.05	5000	0.79536452	FALSE	TRUE	TRUE
0.05	10000	0.79562581	FALSE	TRUE	TRUE

While the presence or absence of RIFA is the main contributing factor to the overall percentage of crickets that survive, the sensitivity to resources plays a larger role than either the presence or absence of hot water management of the RIFA mounds, RIFA's ability to raid caves, or the absolute carrying capacity of the cave. For caves within the foraging radius of RIFA, the robustness of cricket populations to fluctuations of resource availability is a key factor that requires further data collection and analysis.

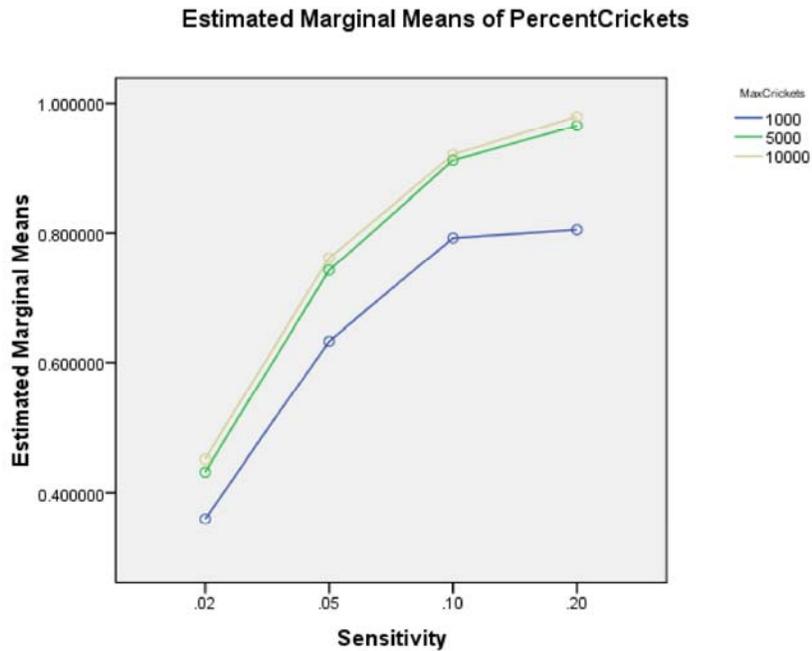


Figure 3. Effect of sensitivity on average level of percent of crickets when RIFA is present.

At any cave size, management of mounds was able to alleviate the decrease in crickets caused by RIFA activity. However, for caves of $K = 1,000$, management was seen to play a much larger role, with the average population size increasing by almost 20% of its maximum (see Figure 4).

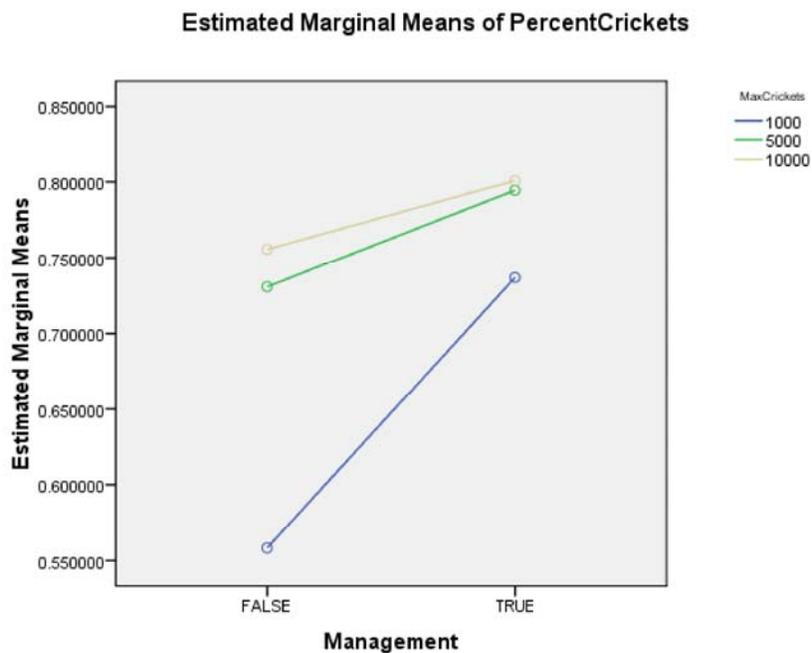


Figure 4. Effect of management on average level of percent of crickets when RIFA is present.

While larger caves do appear to be influenced by yearly hot water treatment of surrounding RIFA mounds, this indicates that smaller caves may be the most cost-effective place to provide RIFA management. This is especially true since the lower average number of crickets present in caves (where $K=1,000$ when no management is present), is due in part to the relatively large number of caves that have lost all their crickets when no management was applied.

With management, the largest average number of caves lost was 0.774, but without management, the largest average number lost was 2.323, as was shown in Table 1.

6 Discussion

NetLogo software is a powerful tool for modeling interactions between various individuals or organisms. It models individual “agents” working within a field made of “patches.” However, when attempting large-scale computations over many iterations, such as environments with too many agents, the program shows significant reduction in speed and usability (Sklar 2007).

The interactions of RIFA and cave crickets involve hundreds of thousands of individuals, making individual interactions between the two species impossible to model using NetLogo. In order to solve this limitation, we used entire caves and RIFA mounds themselves as agents, instead of individual crickets or ants.

These agents then interacted with the environment and with each other on a large scale, depleting resources within 10 m x 10 m patches, and creating a circle of influence based on foraging range and population size. In order to track the population size of a cave or mound, a counter within each agent counted how many individuals were alive.

RIFA are known to be a danger to cave communities (Taylor 2003b). With the RIFA invasion of Fort Hood, Texas (Elliot 1992) cave-dwelling species listed under the Endangered Species Act (USFWS 1994, 2000) are being threatened. However, the simulated model showed that not all caves will be impacted uniformly by RIFA, and additional information about the robustness of cricket populations is vital to understand the scope of impact.

In the simulated model, there were five factors that influenced cave cricket survivorship:

1. presence or absence of RIFA
2. whether or not RIFA raided caves
3. K of the cave, which can be correlated in natural populations to overall cave size and abundance of surrounding resources
4. sensitivity of cricket populations to fluctuations in resource availability
5. presence or absence of the hot water treatment performed on caves within the foraging radius of crickets.

The current model confirmed that RIFA can have a negative impact on cave cricket populations. While this impact varies in severity across many scenarios, there are a significant number of times when it can cause complete cave loss. Even without complete cave loss, the number of crickets can be bottlenecked, causing a reduction in the gene pool. Even the largest caves examined sometimes suffered a loss of over half their cricket population.

With this in mind, there is a need for more research on RIFA and cave crickets within the Fort Hood area, to preserve the species diversity of the cave habitats. Another area for research is the extent to which raiding of cave crickets by RIFA occurs.

Also, since it has been shown that RIFA can impact cave cricket populations, even without raiding, management needs to be applied, even if it is discovered that raiding is more minor than anticipated.

However, raiding did play an important role in complete cave loss. As stated above, a conservative estimate was given for the number of crickets taken by RIFA during raiding, since the exact number is not known, due to difficulties in tracking RIFA raids. If this number is significantly higher, raiding could be a vital part of the problem caused by RIFA, and management techniques that specifically target it will have to be devised.

Still, whatever the number of crickets taken by raiding, this model shows that RIFA impact cave communities, even if raiding ceases.

Cave size was shown to be a major factor in the loss of caves. Despite caves of all sizes having their average percent of the population lowered, the caves with a $K = 1,000$ crickets were the most at-risk for complete loss. This may occur through the lowering of the absolute cricket populations, at which point, either raiding or lack of resources may be the final push to remove all crickets.

When it comes to predicting total cave loss, the number of crickets within a cave (once it has stabilized to a RIFA invasion), is far more important than the number of crickets the cave can hold.

However, the smaller caves are still important, because the 32 caves with the lowest number of average crickets all had a $K = 1,000$, even though

there was a condition where the caves that had a $K = 5,000$ experienced significant cave loss.

However, the average number of crickets left at the end of the simulation was not a direct indicator of cave loss, because the eight conditions where the caves had a $K=1,000$ that experienced cave loss, were not the bottom eight caves with the lowest average number of crickets (Table 3). These caves, and their relative number of complete losses, give patterns that allow the caves to be narrowed down to two groups: those that may experience cave loss, and those that are at high risk for cave loss.

Table 3. Simulation results sorted by the average number of crickets left at the end of the trial.

Sensitivity	Max Crickets	Ave Crickets	Ave Cave Lost	Percent of Max
0.02	1000	186.3145161	2.322580645	0.186314516
0.05	1000	320.766129	1.838709677	0.320766129
0.02	1000	332.9516129	0.774193548	0.332951613
0.2	1000	411.3839286	1.821428571	0.411383929
0.02	1000	439.5241935	0	0.439524194
0.1	1000	442.9375	1.642857143	0.4429375
0.02	1000	480.2419355	0	0.480241935
0.05	1000	658.2016129	0.064516129	0.658201613
0.02	1000	716.09375	0	0.71609375
0.02	1000	716.453125	0	0.716453125
0.02	1000	716.875	0	0.716875
0.02	1000	716.921875	0	0.716921875
0.05	1000	759.1048387	0	0.759104839
0.05	1000	792.8709677	0	0.792870968
0.2	1000	826.6696429	0.142857143	0.826669643
0.1	1000	857.9196429	0.071428571	0.857919643
0.1	1000	918.2678571	0	0.918267857
0.1	1000	950.4375	0	0.9504375
0.05	1000	957.1875	0	0.9571875
0.05	1000	957.25	0	0.95725
0.05	1000	957.2578125	0	0.957257813
0.05	1000	957.265625	0	0.957265625
0.2	1000	987.6160714	0	0.987616071
0.2	1000	995.4732143	0	0.995473214
0.1	1000	998	0	0.998
0.1	1000	998	0	0.998
0.1	1000	998	0	0.998

Sensitivity	Max Crickets	Ave Crickets	Ave Cave Lost	Percent of Max
0.1	1000	998	0	0.998
0.2	1000	1000	0	1
0.2	1000	1000	0	1
0.2	1000	1000	0	1
0.2	1000	1000	0	1
0.02	5000	1801.064516	0.096774194	0.360212903
0.02	5000	2175.975806	0	0.435195161
0.02	5000	2217.774194	0	0.443554839

While complete cricket loss is slightly correlated to average number of crickets ($r = -0.504$, indicating that as the average number of crickets goes down the likelihood of cave loss goes up), there are many conditions with no cave loss that have fewer average crickets than some conditions with some cave loss. A lower average number of crickets puts caves at risk for complete cricket loss, but is not an absolute indicator that caves will be lost.

Caves with a population averaging below 500, when RIFA are present, can be considered at high risk for cave loss. Caves under these conditions often experienced complete loss of crickets, with over 5 out of 7 conditions experiencing complete loss of crickets. This loss occurs regardless of the sensitivity crickets have to their resources, if the RIFA are directly raiding the caves, or if management techniques are in place (although management can be seen to alleviate the number of caves lost).

Conditions where the caves have an average population of more than 500 crickets still show some caves loss, though it drops off drastically, with 0.14 average caves lost being the largest number of caves that lose all crickets. However, there are still possible losses of caves all the way to those having an average population of 2,000 crickets. Despite a relatively robust level of survivorship, these caves also appear to be at risk of cricket loss from RIFA.

In light of this finding, it may be most cost effective for Fort Hood to identify smaller caves that contain fewer crickets, and concentrate efforts on management of these communities. This is especially true of caves that are exposed to RIFA, and have a population of 500 crickets or less.

While RIFA also appeared to impact the caves that have larger cricket populations, (in some cases lowering their populations to 40% of their K), those caves appeared to settle at a new, lower population without risk of complete cricket loss. Efforts to reduce RIFA foraging close to these caves may not be a cost-effective method for conserving the endangered species within the cave ecosystems on Fort Hood.

Conversely, smaller caves appear to be impacted greatly, and are in need of at least yearly hot water treatments to surrounding RIFA mounds. In many cases, even this treatment may not be enough, and more aggressive management measures may need to be taken.

Sensitivity to surrounding resources was also a factor in the survivorship of cave cricket populations. Unfortunately, it is not known how sensitive crickets are to fluctuations in resource availability. Nor is this a factor that can be controlled for, such as focusing on caves with smaller cricket populations. Instead, new research needs to focus on how cricket populations fluctuate with resource availability, and the amount to which this availability is changed by the addition of RIFA.

However, until this information is obtained, management techniques need to be aggressively applied to all caves with small cricket populations, and at least yearly spot treatment performed for caves of moderate cricket population.

In this way, the current model has left two directions that need to be taken. It shows that more information needs to be gathered on the cave crickets, specifically on how they react to changes in food availability. This information is pertinent to assessing which caves need to be protected from RIFA, and how aggressively they need to be protected. Depending on the crickets' sensitivity to their food availability, some caves may not need protection, or additional caves may need to be managed. At the same time, the model shows us the potential impact of RIFA on cave communities – working through the impact on cave crickets – that demands immediate management to stop possible species loss.

It has been shown that a simple hot water treatment can be effective in reducing loss of cave species in most caves. Yet, it has also been shown that more aggressive treatment needs to be applied to smaller caves until more is learned about how these caves will react to changes in resources. At that

time, we may find that water treatment is still effective, or that more management is needed to protect the endangered karst invertebrates.

This discussion highlights some of the limitations of this model. While some parameters were accounted for through multiple iterations that assigned different values (sensitivity to resources being one of these), others had to be estimated to simplify the model enough that it could be run. Among these, and related to sensitivity, is the question of how quickly resources become depleted by each species.

While resources are not so abundant that they play no role in regulating population size, it is not known exactly how fast they are used up. Nor is it known how fast they are replenished through new growth, influx of new prey species, or through other means. It is likely that this rate of replenishment also will change, based on the season. Future versions of the model should account for various rates of growth during each season.

The season may affect the overall populations of RIFA mounds. There has been evidence that RIFA populations reach their maximum numbers in midwinter, their maximum biomass in the spring, and declined to a minimum in midsummer (Tschinkel 1993). However, it can be difficult to track exact numbers of RIFA, as they may be foraging more underground to avoid heat during the summer, or may have multiple queens sharing control over one colony with multiple mounds, the latter known as polygyne colonies (Taylor 2008).

To simplify control methods, this simulation ran the most common method for exterminating RIFA – hot water treatment. Other options are available, however, including pesticides, poison bait, and the imported phorid fly. While each of these pose their own risk, they have all been used to some degree, and it would be beneficial to understand the impacts of these methods on baits.

One problem with all control methods is the method of application. Unfortunately, most of the areas in need of management do not have easy access for humans. As such, bringing in equipment to control the RIFA causes disturbances, which might aid RIFA colonization.

For example, bringing in boiling water to kill RIFA mounds involves a truck with a large bed to hold a water boiler, hoses, and other equipment.

Driving this to the area of interest will uproot vegetation and soil, allowing for RIFA to more easily access the area. The truck must also drive around to each RIFA mound, uprooting more vegetation and soil in a wide area around the cave, possibly making it very easy for RIFA to colonize the entire area around the cave.

Obviously, this would be a counter-productive way to save the endangered karst invertebrates. To understand this, future versions of the model will have disturbances created from a set point to the caves and surrounding region during each treatment session.

Because of the adverse effects associated with disturbances, extreme care must be made when assessing and managing the caves of interest. Caves first need to be measured for their size (and, more importantly, for their cave cricket population), without bringing in large vehicles to do so. Similarly, if a small cave cricket population is identified in a cave with endangered species, the management must be even more careful not to disturb the surrounding land to too great of an extent. At the same time, if RIFA are present, aggressive management needs to be applied immediately to the RIFA mounds surrounding caves of interest.

7 Conclusions and Recommendations

7.1 Conclusions

The RIFA model documented here serves as a demonstration of a new cost-effective approach that natural resource personnel may use to rapidly combine their knowledge of environmental and ecological processes with GIS-enabled digital maps to create spatially explicit models.

It has been demonstrated that, using the freely available NetLogo modeling environment, ecologists can quickly learn to capture their individual expertise about an environment as formal statements that can drive a realistic simulation model. No specialized programming skills are required by the model developer. The RIFA model documented here was developed by three graduate students working quarter time over 4 months. Their tasks were to research the RIFA technical literature, communicate with Fort Hood ecologists and RIFA experts, learn how to use NetLogo, capture the results in a model, and prepare associated reports and presentations. The ecology researchers were able to independently develop, own, understand, and “own” the resulting RIFA model without intervention by a computer programmer.

The RIFA model developed for this study was created for use in the public domain, and may be downloaded from <http://earth.cecer.army.mil/SARPVA> at no charge, for adoption or adaptation by natural resource managers working within RIFA territories. Although this model was developed to capture interactions among RIFA colonies and cave cricket populations associated with Fort Hood caves, the model can be easily modified to address RIFA management questions at other locations.

7.2 Recommendations

Based on the findings from the presented model, the following recommendations are offered.

7.2.1 Management

1. Cave ecosystems that rely on cave cricket populations need to be identified and assessed. The locations of these caves and the types of surrounding environment (e.g., disturbed or not, relative abundance of re-

- sources) need to be recorded, along with recording the population of crickets within the cave, and the presence or absence of RIFA.
2. Caves that have RIFA present will need management at different levels, depending on the cricket population present.
 - a. Caves with a population of 500 or fewer crickets need immediate protection. All surrounding RIFA mounds should be treated with hot water, and treatment should continue regularly on any new RIFA mounds that appear. The caves should be monitored to assess the health of the cricket population.
 - b. Caves with a population of 2,000 crickets, that also have RIFA present, should have their RIFA mounds treated with hot water on a yearly basis, at minimum.
 - c. Caves with a population of 1,000 crickets, but that do not yet have RIFA present, need to be monitored closely to see if any RIFA invade the habitat. If RIFA invade, they need to be managed on a yearly basis, while watching cricket populations to see if more management is required.
 - d. Caves that have a population of 5,000 crickets, with no RIFA present, should be inspected on a yearly basis to see if RIFA invade, and, if so, how the population is affected.

7.2.2 Research

1. The impact of RIFA invasions on resource availability needs to be documented. This includes the amount of pertinent resources that are depleted from the environment and how fast they are replenished, as well as the degree to which the presence of RIFA discourages cave crickets from foraging in the same area.
2. The impact of food variation on cricket populations needs to be better understood. Research must be carried out to quantify how much of a decrease is seen in the cave cricket population for a given decrease in food availability. Combined with the above research, this will allow for the quantification of the indirect impact of RIFA on cave crickets.
3. The extent to which raiding occurs in caves at Fort Hood needs to be documented. This is perhaps the hardest variable to assess, as caves can have entrances and exits that are too small for humans. However, it has an important impact on the cave populations. While raiding was not a strong factor in decreasing the average number of crickets within a cave, it played a strong role in those that experienced complete cricket loss. It is possible for raiding to be the final blow that causes cricket populations to drop to a level from which they cannot recover,

once the population has been sufficiently lowered through other, indirect methods.

7.2.3 Applications

1. Prospective users of the RIFA model are encouraged to extend and further develop the basic model to meet their specific needs. The model can be augmented with any location-specific data available pertaining to the impacts of weather patterns or climate change, cave microclimate, karst species distribution, number of queens in the RIFA colony, etc.
2. Installation biologists and land managers are encouraged to consider investigating the use of small, expedient applications such as the RIFA model presented here. Even small, quickly developed models can provide users with practical, analytically sound decision support during the discussion of land management policy alternatives.

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