

BURROWS OF SEMI-FOSSORIAL VERTEBRATES IN UPLAND COMMUNITIES OF
CENTRAL FLORIDA: THEIR ARCHITECTURE, DISPERSION AND ECOLOGICAL
CONSEQUENCES

By

ALTON EMORY KINLAW

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

2006

To my daughter Skye Gabrielle Kinlaw, who has accomplished
more in her short 11 years than most adults do in a lifetime.

ACKNOWLEDGMENTS

I owe a major professional and personal debt to my chair, Michael Moulton for his guidance. In particular, at a time when I was discouraged due to health and financial reasons, he encouraged me to stay the course. Because of his quantitative background in orthithology, herpetology, and mammalogy, he has a unique intellectual perspective about vertebrate ecology and always challenged me to ask the right questions. Additionally, he provided me with a balance, Sherman live traps, and microscope.

My co-chair, Dick Franz, shared his comprehensive knowledge about natural history of Florida fauna, and served as project director of the Avon Park project issues. He encouraged me to write the Avon vertebrate diversity chapter and carefully critiqued all of my papers.

My research is based upon the theoretical background developed by Jim Nichols and his colleagues at Patuxent Wildlife Research Center. Jerry Butler, UF Department of Entomology and Nematology, provided sticky traps and “Tick Sucker” vacuums, reprints, and freely shared his extensive knowledge of insect fauna that use tortoise burrows. Ken Portier graciously stayed on my committee after leaving UF for a position in Atlanta, and allowed me to visit him with my questions. Katie Sieving always provided thoughtful advice. Willie Harris, UF Department of Soil Science was the visionary who encouraged me to think of the subsurface soil layer as a three dimensional life environment, and this ultimately led me to conduct the ground penetrating radar investigations.

Sam Jones provided equipment and a truck and helped in many ways during the early part of my field work. George Tanner loaned me an ORV during the early part of my field work.

Thanks are extended to W.R.J. Dean, Joel Brown, and Fenton Kay for critically reviewing the material in chapter 2.

The Avon Park research was supported by the Natural Resources Flight of the Avon Park Air Force Bombing Range (Project RWO-169). Pat Walsh assisted with many operational aspects of the field work, and Peg Margosian provided valuable GIS support. I thank the Florida Cooperative Wildlife Research Unit for its assistance in managing the funds used for the Avon Park research.

For the gopher tortoise chapter, I thank the members of the survey team: Dick Franz (Director), Rex Kinlaw, Kenny Koehler, Richard Bubba Owen, Chris O'Brien, David Maehr, and Lora Smith.

For the armadillo chapter, a special debt of gratitude is owed Gary White, who both provided the SURVIV code he used in the White and Bennetts (1996) paper and corrected my SURVIV code. C. Krebs answered questions about his computer program. Marinela Capanu, Department of Statistics, IFAS, University of Florida, provided statistical support. Jennifer Brown shared information about her possum simulation study in New Zealand. James Layne reviewed an early draft of the manuscript. C. Krebs answered questions about his computer program. Colleen McDonough clarified plot data from her north Florida study.

For the burrow architecture chapter, Jerry Fensch of Florida Environmental allowed me to foam tortoise burrows in a tortoise relocation project near Clermont, and made arrangements for a backhoe to dig the burrows up. Larry Conyers, University of Denver, and Mark Grasmusen, University of Miami, brought their ground penetrating radar equipment to my study area for the radar survey.

For the Avon Park vertebrate diversity chapter, Dick Franz, Bubba Owen, and Chris O'Brien identified many of the specimens. Dick Franz and Bubba Owen provided slides and clarified aspects of the sampling process. Kenny Krysko provided access to his unpublished range maps of herpetofauna of Florida.

For other aspects of my research, the following biologists (and their affiliation) provided access to the following study areas: Anne Malatesta (Lake Wales Ridge State Forest); Boyd Blihovde and Bubba Owen (Wekiwa Springs State Park), Carlton Hall (Dynamac Corporation, Kennedy Space Center) and Marc Epstein (Merritt Island National Wildlife Refuge), the natural resources staff at Ocala National Forest, especially Janet Henshee.

Bob Giguere, Executive Producer of WMFE Channel 24 in Orlando, filmed my project as part of his documentary, "Wekiwa-Legacy or Lost?" Herb Kalmbacker (IFAS) loaned me seed shakers. Dave Almquist, Entomology, shared his knowledge regarding beetle taxonomy and his "burrow facade trap." Louis Kelemen of Zelwin Farms built a small "tick sucker" vacuum for me, and Bill Kelly provided me with many sources for the many supplies I needed. Paul Schumacher of Hughes Supply, Inc of Orlando not only provided 8 and 10 in PVC pipe (for pitfall traps) gratis, but spent time cutting sections for me.

My wife Monnie, while not a biologist, had an uncanny sense for what would and would not work with my traps. Her background as an agricultural nurse proved to be helpful in uncountable ways, especially with my history of Lyme disease. My daughter Skye was a very colorful and chatty field assistant on several occasions, and enthralled everyone with her comments about "getting dirty as a pig."

TABLE OF CONTENTS

	<u>page</u>
ACKNOWLEDGEMENTS.....	3
LIST OF TABLES.....	9
LIST OF FIGURES.....	11
ABSTRACT.....	14
 CHAPTER	
1 INTRODUCTION.....	16
2 A REVIEW OF BURROWING BY SEMI-FOSSORIAL VERTEBRATES IN ARID ENVIRONMENTS	19
Introduction: Fauna of Arid Regions	19
Methods.....	20
Results and Discussion.....	21
Natural History.....	21
Functional Ecology, Burrow Architecture, and Burrowing Behavior.....	25
Classical Ecological Issues.....	31
Animals as Engineers and Resulting Impacts...	33
Geomorphology.....	36
Pedological Effects of Burrowing on The Soil.....	37
Pedological Effects of the Soil Type on Architecture and Species Distribution.....	38
Vegetation Effects.....	39
Animal Community Ecology.....	39
Future Research and a Conceptual Model	41
3 SAMPLING APPROACHES TO ESTIMATE DENSITY OF GOPHER TORTOISES (<i>Gopherus polyphemus</i>) IN CENTRAL FLORIDA	46
Limitations of Current Gopher Tortoise Burrow Census Methods.....	46
Materials and Methods.....	50
Results.....	55
Discussion.....	57

4	BURROW DISPERSION OF ARMADILLOS (<u>Dasyus novemcinctus</u>) AT AVON PARK AIR FORCE RANGE, FLORIDA	70
	Introduction: Armadillo Life History.....	70
	Study Area.....	72
	Methods.....	72
	Results.....	76
	Discussion.....	77
5	ARCHITECTURE OF GOPHER TORTOISE BURROWS DETERMINED BY 2D GROUND PENETRATING RADAR.....	86
	Introduction: Gopher Tortoise Burrows.....	86
	Ground Penetrating Radar Methodology.....	87
	Field Site Description and Burrow Selection.....	88
	GPR Collection Procedure.....	90
	ImageAnalysis.....	93
	Results.....	94
	Discussion: Advantages and Limitations of GPR.....	95
6	BIOLOGICAL APPLICATIONS OF FULL RESOLUTION 3D GROUND PENETRATING RADAR IMAGING.....	105
	Introduction.....	105
	Methods.....	105
	Results.....	106
	Discussion.....	106
7	OCCUPANCY OF FAUNA INHABITING GOPHER TORTOISE BURROWS LOCATED IN SCRUB AND SANDHILL VEGETATION OF CENTRAL FLORIDA.....	116
	Introduction.....	116
	Study Areas.....	117
	Sampling Methods.....	118
	Results.....	121
	Discussion.....	122
8	VERTEBRATE SPECIES RICHNESS AT AVON PARK AIR FORCE RANGE, FLORIDA ESTIMATED WITH THE JACKKNIFE.....	139
	Introduction: Species Richness Estimation	139

Methods.....	143
Results.....	144
Discussion.....	144
True Presence (True Positives).....	144
False Positives	145
True Negatives	145
False Negatives and Detection Probability.....	147
Availability.....	148
Sampling Bias of Methods Used.....	151
Species Missed Due to Inappropriate or Insufficient Methods.....	152
Species Characteristics, including Rareness.....	154
When is a Species “Effectively Not There”?.....	155
Conclusion.....	157
9 SUMMARY.....	166
LIST OF REFERENCES.....	169
BIOGRAPHICAL SKETCH.....	194

LIST OF TABLES

<u>Table</u>	<u>page</u>
2-1	Diversity of animal fauna found in burrows in semi-arid environments or environments with dry, sandy soils.....43
3-1	Summary statistics for Gopher Tortoise burrow quadrat study conducted in four upland habitats at Avon Park Air Force Range, 1997-98.....62.
3-2	Likelihood ratio tests comparing four negative binomial models of tortoise burrow dispersion to determine if differences exist in m , k , or both.....63
4-1	Summary statistics for armadillo burrow study in four upland habitats at Avon Park Air Force Range, 1997-98.....80
4-2	Likelihood ratio tests comparing the initial four models of armadillo burrow dispersion to determine if differences exist in m (mean), k (clumping parameter), or both.....81
4-3	Log-likelihood, G statistic for goodness of fit, degrees of freedom of G (probability $> G$ is denoted by P), and Akaike Information Criteria (AIC) scores for each of the four initial models used in armadillo study.....82
5-1	Data for gopher tortoise burrow study collected without and with ground penetrating radar.....99.
6-1	Statistics on four Gopher Tortoise burrows at the Kerr sandhill site, Ocala National Forest, collected with full-resolution 3D ground penetrating radar.....109
7-1	Number of occasions that all vertebrates seen in the study were captured or observed at the burrow entrance or at a matching bucket trap in the burrow study.....126
7-2	Naïve and model estimates of occupancy (ψ) and detection probability (p) computed with program Presence for Gopher Frogs and Florida Mice inhabiting Gopher Tortoise burrows in the scrub and sandhill communities of Central Florida during July-November, 2005.....127.

7-3	Summary of models fit to Gopher Frog and Florida Mice occupancy data collected at Gopher Tortoise burrows during July-November, 2005.....	128
7-4	Occupancy and detection probabilities for Gopher Frogs and Florida Mice co-occurring in Gopher Tortoise burrows in scrub and sandhill communities of Central Florida during July-November, 2005.....	129
7-5	Microsoft Excel spreadsheet of tick data for individual burrows from the Kerr plot for the 5 month period, July-November, 2005.....	130
8-1	Sampling Methods and Intensities for 2 Surveys of Vertebrates at Avon Park Air Force Range, FL. during surveys by Branch and Hokit (2000) and Franz et al. (1998).....	159
8-2	List of vertebrates recorded at Avon Park Air Force Range, Florida (APR) during three separate surveys from 1988-1998.....	160
8-3	“Candidate” vertebrates that could potentially occur at Avon Park Range, FL, but were not recorded during three surveys from 1988-1998.....	163
8-4	Sampling methods, effort, rarity that could have been detected, and binomial upper 95%confidence intervals for species detected zero or only a few times during two surveys conducted at Avon Park Air Force Range, FL, from 1994-98.....	165

LIST OF FIGURES

<u>Figure</u>	<u>page</u>
2-1 Complexity of burrows dug by three rodents in soils with varying soil textures.	44
2-2 Conceptual model of landscape-level effects of burrow systems.....	45
3-1 Gopher tortoise (<u>Gopherus polyphemus</u>) walking.....	64
3-2 Contour map of Avon Park Air Force Bombing Range.....	65
3-3 Location of random 1 hectare plots along the Frostproof Road area of Avon Park Air Force Range during quadrat study, 1997-98.....	66
3-4 Frequency count of gopher tortoise burrows surveyed in arid oak scrub versus count expected by the negative binomial distribution.....	67
3-5 Bias of extrapolated population estimate of active tortoise burrows in 1762 hectares of oak scrub habitat.....	68
3-6 Effect of clumping of burrows on precision of sample abundance estimate in a quadrat sampling survey at Avon Park Air Force Range, Florida.....	69
4-1 Nine-banded armadillo foraging.....	83
4-2 Graph of frequency count of armadillo burrows at Avon Park Air Force Range, FL, in 1997-98 in four upland habitats.....	84
4-3 Graph of the actual pine data to that expected by the negative binomial distribution	84
5-1 Pulling GPR antenna in perpendicular direction across the long axis of a gopher tortoise burrow in a sandhills plant community, Ocala National Forest, FL.....	100
5-2 Two dimensional profile of burrow Kerr6 on ground surface	100

5-3	Hyperbole (indicated by arrow) shown in GPR reflection profile, collected by moving the GPR antenna on the ground surface over the burrow at a 90 degree angle to the orientation of the burrow.....	101
5-4	GPR longitudinal profile of burrow, collected by moving the GPR antenna on the ground surface following the path of the burrow.....	102
5-5	Three dimensional image of burrow Kerr3 developed using the Slicer-Dicer isosurface modeling program.....	103
5-6	Black on white three dimensional rendering of burrow Kerr6 developed with the FormZ program.....	104
6-1	Survey plan for 3D GPR surveys in January, 2006, at Kerr site, Ocala National Forest.....	110
6-2	Three dimensional image of burrow Kerr1.....	111
6-3	Three dimensional image of burrow Kerr2.....	112
6-4	Three dimensional image of burrow Kerr3.....	113
6-5	Three dimensional image of burrow Kerr4.....	113
6-6	Validity of 3D GPR imaging over 2D GPR at burrow Kerr2.....	114
6-7	Comparison of 4 Kerr burrows, top view (looking down into the ground).	115
7-1	Six trapping methods attempted early in study.....	131
7-2	Combination trap.....	132
7-3	Malaise and experimental traps.....	133
7-4	Overall trapping effort at burrow entrance, categorized by number of traps set per method.....	134
7-5	Number of traps in which vertebrates were caught at the burrow entrance with pitfall or Sherman traps or by observation.....	135

7-6 Comparison of the number of individual vertebrates captured at the entrance to Gopher Tortoise burrows in pitfall traps, Sherman traps, and by observation.....136

7-7 Invertebrates captured on more than 50 occasions during burrow study in scrub and sandhill communities in Central Florida.....137

7-8 Invertebrates captured on less than 50 occasions during burrow study in scrub and sandhill communities in Central Florida.....138

Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

BURROWS OF SEMI-FOSSORIAL VERTEBRATES IN UPLAND COMMUNITIES OF
CENTRAL FLORIDA: THEIR ARCHITECTURE, DISPERSION AND ECOLOGICAL
CONSEQUENCES

By

Alton Emory Kinlaw

December 2006

Chair: Michael Moulton

Cochair: Richard Franz

Major Department: Wildlife Ecology and Conservation

This research centers on the role of burrows excavated by vertebrates in upland communities of Florida. I summarized the fragmentary literature on the subject into a coherent and synthetic review. I quantified the dispersion of burrows of the gopher tortoise and armadillo at Avon Park Air Force Range, showing that both species fit the negative binomial distribution, indicating aggregation. Oak scrub had the highest density of tortoise burrows per hectare and pine flatwoods the highest density of armadillo burrows. A camera survey of burrows in oak scrub showed a 67% occupancy rate of tortoises, yielding a population point estimate of 1761. Gopher Tortoise burrows were imaged for the first time in 2005 using 2D ground penetrating radar. Three dimensional imaging programs showed that tortoises dig burrows in a downward spiral resembling a corkscrew. In 2006, the burrows were imaged again using 3D full resolution ground penetrating radar which showed circular Florida Mouse tunnels intersecting the tortoise burrows, and relict “ghost” burrows nearby. To determine the diversity of species found in gopher tortoise burrows, I sampled 1502 burrows at 3 scrub and 3 sandhill sites in Central Florida from 2000-2005. I used a multi-

sampling approach using pitfall traps, Malaise traps, and a vacuum, and found species representing 24 orders, classes or families of invertebrates and 18 species of vertebrates using the burrows. I computed the probability of occupancy for the Gopher Frog and Florida Mouse with program Presence. For the frog the values were 0.91 and 0.25 for the sandhills and scrub, respectively, and for the mouse the respective values were 0.27 and 0.65. The best fitting model was one in which occupancy and detection probability of each species was independent. I analyzed three ecological surveys conducted from 1988-98 for vertebrates at Avon Park Air Force Range using the jackknife estimator. The count of observed species was 94 and the predicted estimate with the jackknife estimator was 108 ± 5.3 , indicating that between 9 to 19 species were “missed.” I provide explanations for the missing species and compute the rareness that could have been detected given the sampling intensities used.

CHAPTER 1 INTRODUCTION

The research presented in this dissertation centers around burrows that vertebrate animals dig in the ground. Chapter 2 presents a literature review of burrows of semi-fossorial species in arid environments around the world. This provides the ecological background for interpreting the information in the chapters to follow.

In Chapter 3 the spatial dispersion of tortoise burrows is quantified. Using a random sampling scheme, the burrows of this species were determined to be aggregated in the oak scrub community, but little so in pine or unburned, overgrown sand pine scrub. Previous workers had suspected a clumped pattern but never quantified it; this is the first to demonstrate that the burrows fit a negative binomial distribution. Additionally, since tortoises sometimes dig their burrows in situations where a common field technique, distance sampling, cannot be used, I present a method to census burrows in those situations. Additional new information presented in this chapter is a population estimate of gopher tortoises for the Avon Park military installation.

In Chapter 4, burrow dispersion for the nine-banded armadillo is quantified. Although this recent invader to Florida will use tortoise burrows, it is unclear if they drive out the tortoises or simply use abandoned burrows. Thus, information is critically needed regarding the density of burrows of armadillos at sites where they overlap with tortoises. I also show that basing a census of a local population of armadillos on a count of its burrows is not feasible.

Chapter 5 presents three-dimensional images of gopher tortoise burrows collected using ground penetrating radar (GPR) in scrub and sandhill plant communities of Ocala

National Forest. This is new information, as these are the first such clear, intact images of the architecture of these burrows ever obtained; previous methods relied on excavation, with unclear interpretation. This species is considered a keystone species, since so many other vertebrates and invertebrates depend on its burrows for shelter. Thus, basic biological information such as this can assist in conservation of an entire assemblage of species using these burrows. A follow-up study (Chapter 6) using a new and sophisticated GPR technology called full resolution 3D imaging provided the dramatic animations and extraordinary detail regarding the underground burrows and the adjacent burrows associated with the main tunnel, allowing me the opportunity to discuss possible ecological consequences of such a system.

There is a common perception in the Southeastern U.S. that gopher tortoise burrows are biologically rich in species. Except for the study by Knizley (1997), previous workers had each used only one method to sample the burrows, so this perception was based on piecemeal information. I conducted a multi-sampling study at three scrub and three sandhill sites in Central Florida from 2000-2005 (Chapter 7). Although some analyses are incomplete, I was able to determine that about 60-70 species use the burrows. Additionally, I was able to compute the occupancy of the imperiled Gopher Frog and the Florida Mouse in these two habitats, critical new information that may assist in the conservation plans for these species.

In Florida and the southeastern United States, ecological surveys are commonly undertaken to determine what species occur in an area. The results of such a survey are usually presented as a list of species observed at a state or federal park, forest, reserve, etc. The more comprehensive the methods and time spent in these surveys, the better the results. At Avon Park Air Force Range, three surveys have been conducted for vertebrates and two of them were very extensive. In Chapter 8, I illustrate how the observed count of species from

these surveys is inevitably an underestimate, by using the probabilistic jackknife estimator. I explore three possible explanations for this: a geomorphological, a distributional, and a sampling explanation.

CHAPTER 2
A REVIEW OF BURROWING BY SEMI-FOSSORIAL
VERTEBRATES IN ARID ENVIRONMENTS

Introduction: Fauna of Arid Regions

Arid regions occupy more than one-third of the earth's land surface. These regions are defined as areas in which potential evapotranspiration greatly exceeds precipitation during most of the year (Buol et al. 1997). Different vertebrates have evolved various physiological, morphological, and behavioral adaptations to cope with this aridity. One important adaptation is burrowing, which provides a means to escape the hot, dry surface conditions. Although animals burrow in other eco-regions, the possession of a cool, moist burrow with stable temperatures underground is especially critical for survival in arid zones that are hot and dry with greatly fluctuating temperatures on the surface. The burrowing habit in vertebrates evolved as early as the Carboniferous (Olsen and Bolles 1975) and may have been responsible for the success of many early life forms of the animal kingdom; certainly this represented the first type of "shelter." Moreover, burrowing species can be found across taxonomic and community boundaries worldwide. Depending on the species that excavates, the burrow can vary greatly in diameter, depth, and complexity. Moreover, burrows can impact geomorphology, hydrology, soil dynamics, vegetation patterns, and animal community diversity at scales ranging from microsites to landscapes. Burrowing is just one of a series of activities such as trampling, wallowing, digging and geophagy that can have tremendous impacts on the landscape (Taylor 1935, Jacob 1940, Thorp 1941, Abaturvov 1972, Hole 1981, Meadows and Meadows 1991, Stone and Comerford 1994, Butler 1995). For these reasons, this phenomenon deserves study in its own right.

In this review, I focus on burrows open to the surface dug by semi-fossorial vertebrates. The intent here is to present an overview of the rich variety of research conducted on vertebrate burrows but not necessarily to provide a comprehensive research agenda for the future.

Methods

I searched numerous data bases (Biological Abstracts, Agricola, Zoological Record, Wildlife and Fisheries Abstracts) for journal articles, books, dissertations, and theses related to burrowing and the impact of burrowing. I categorized papers into artificial divisions, depending on the primary focus of the paper reviewed and these divisions are not mutually exclusive. The categories I chose were natural history, ecological theory, and the traditional academic disciplines of geomorphology, soil science, plant science, and animal community ecology. The last approach is preceded with a discussion of the burrowing phenomenon as an “animal-engineering” process.

These data bases only abstract the literature from recent years and not the early primary literature. My review is not exhaustive, but it fulfills my goal to provide an overview of burrow research. The emphasis is on the ecology of semi-fossorial vertebrates, not true fossorial species. Much of the extensive Russian literature was not translated and the review is biased towards papers written in English. Relevant citations dealing with non-arid environments were also included. Investigations centering on physiology or genetics were not included. Finally, only a sampling of the available citations involved with each topic below is discussed.

Results and Discussion

Natural History

The principal burrow excavators are the mammals, who often can construct very elaborate, complex burrows with many forks and chambers. Of 777 genera of terrestrial mammals listed in Walker (1968), 447 are potentially significant in soil disturbance, and 58% of this 447 do so by surface feeding accompanied by burrowing (Paton and Humphreys 1995). All 3 orders of reptiles include members that spend time underground by either using tunnels built by other animals (Halliday and Adler 1986) or by actively excavating their own. Research describing the natural history of this “digger/hole” system usually focuses on the primary excavator or the resulting burrow.

I categorize primary excavators (“tunnelers”) as species in which digging plays the major role in their existence. These are strong and accomplished burrowers who dig a tunnel into the soil or into a bank. These excavations can be extensive in length and size, are open at the ground surface, and can have major environmental impacts. The epitome of this category would be the armadillo or antbear (Orycteropus afer) in southern Africa, which can excavate burrows spacious enough such that a bovid (the steenbok, Raphicerus campestris) can rest in the entrance (Smithers 1971). The plains vizcacha (L. maximus) in Argentina digs very large, complex burrows with many openings (Mares et al. 1989), as does the prairie dog (Cynomys leucurus, Sheets et al. 1971) in North America. Primary excavators on a smaller and simpler scale are the Testudinidae of North America, whose distribution (Goin et al. 1962) overlaps much of the distribution of aridisols (Buol et al. 1997). The burrows of these tortoises are comparatively simple but can be deep.

Secondary modifiers are vertebrates that inhabit and secondarily modify a burrow dug by a primary excavator. Mammals that are secondary modifiers are often capable of digging their own burrows in soils of lower density but are stopped by a hard pan (e.g., the rabbit, Oryctolagus cuniculus in Australia, Parer et al. 1987, the ground squirrel Ictonyx striatus in Orange Free State, Lynch 1983). Eastern cottontail rabbits of Florida (Sylvilagus floridanus) often are found in inactive gopher tortoise (Gopherus polyphemus) burrows in excessively drained thick sands in xeromorphic shrub scrub where they frequently modify the opening (pers. obs.). Greer (1989) lists species of Australian Gekkonidae that use the burrows of spiders or other lizards, but plug the burrows with dirt. In Arabia the ground gecko, Bunopus tuberculatus, starts burrowing within the burrow systems of desert rodents (Arnold 1984) and the small pygmy gerbil (Gerbillus nanus) frequently begins its digging activities within the warrens of larger rodents (Kingdon 1990). Some snakes are known to modify burrows by forceful serpentine movements.

A third category would be simple occupants of the burrow who play no role in digging the structure but simply take advantage of its existence. To continue the Florida example, species in this category would be many invertebrates such as silphid beetles (Silphidae), various reptiles (Anolis carolinensis), and even birds (Colinus virginianus) all of which utilize tortoise burrows (Cox et al. 1987).

Burrow inhabitants frequently found in a certain type of burrow are referred to as commensals. Commensals are further classified into obligate (only found in that particular burrow type) versus non-obligate categories such as “occasional,” “frequent,” “accidental”; the latter three imply that the inhabitant might just as likely use some other type of shelter. While obligates may use another type of shelter for rest or reproduction, it is usually not

optimal; since the obligate has a co-evolutionary history with the primary excavator. Uma exsul, a desert dwelling lizard, is restricted to areas in which rodents can maintain open burrows year-round (Pough et al. 1978). The distribution of gopher frogs (Rana capito) in Florida is restricted to the distribution of gopher tortoises, where the frogs use the burrows as retreats (Godley 1992). Butts and Lewis (1982) found that 66 % of burrowing owls (Athene cunicularia) surveyed in Oklahoma, USA, were found in black-tailed prairie dog (Cynomys ludovicianus) burrows, even though the prairie-dog towns only occupied 0.16% of the area. They believed that owls nesting in non-prairie dog areas were utilizing marginal habitat (however see Haug et al. 1993).

Authors frequently classify burrows according to the apparent function they serve for the user. An early example from the literature is Steiniger (1949, 1950, 1952) for Norway rats (Rattus norvegicus): a home burrow used for residence; a food storage burrow located near food sources; and a refuge burrow, found near foraging areas. Turner (1972) classified three types of escape burrows used by Belding's ground squirrel (Spermophilus beldingi): short burrows with one entrance, intermediate length burrows with two or three entrances and long complete burrows. Each is used in response to different alarm calls. Desert tortoises (G. agassizii) use two kinds of burrows: winter dens, usually 8-10 feet deep in banks of washes; and summer dens, a shallow tunnel dug into the base of an arroyo wall (Ernst and Barbour 1972). Other examples can be found in Shenbrot et al. (1997) for G. dasyurus (complex burrows with a nest and simple burrows without a nest) and Rogovin et al. (1996) for Pygeretmus pumilio (day burrows and shelter burrows). Although these classifications may be useful for explaining species-specific biology, they might overlook the possibility that

different parts of the same burrow might be used for different reasons (cf. Burns et al. 1989 for prairie dogs).

The morphological adaptations for burrowing are described in a number of papers. Gekkonid lizards (Diplodactylinae and Gekkoninae) that burrow in the compacted sand of windward dune faces of deserts have webbed feet, used as “sand shovels” (Bauer and Russell 1991). Lizards in Arabia have digital fringes which act like snow shoes, which prevent sinking in the sand but also help with digging (Arnold 1984). An important adaptation in burrowing snakes is the fusion of the brille and postocular; this character was used to re-describe the African colubrid Elapocalamus gracilis Boulenger by Resetar and Marx (1981).

The actual burrowing behavior is not as often described. The arid-dwelling bullsnake (Pituophis melanoleucus) exhibits head morphology and stereotyped motor patterns adapted to excavating. Spading actions by the snout are followed by scooping a load of sand in a head-neck flexure, moving posterior, and dumping the load away from the excavation at varying distances. An excavating bullsnake can move as much as 3,400 cm³ of sediment per hectare (Carpenter 1982). The desert tortoise (G. agassizii) digs by scraping alternately with the forelimbs. When the hole becomes deep enough the turtle turns around and pushes the dirt out with its shoulders (Ernst and Barbour 1972).

A number of papers examine attributes of burrows in semiarid zones, including below ground features such as geometry, complexity, and depth [Clark (1971) for white-tailed prairie dogs, C. leucurus in Wyoming; Flosser (1984), for hairy-nosed wombats, Lasiorhinus latifrons in Australia; Reynolds and Wakkinen (1987), for deer mice, Peromyscus maniculatus, California voles, Microtus montanus, Ord’s Kangaroo rat, Dipodomys ordii, and Townsend’s ground squirrel, S. townsendii in southern Idaho; Hatough-Bouran (1990)

for the lesser Egyptian jerboa, Jaculus jaculus and Wagner's gerbil, G. dasyurus in Jordan; Bronner (1992) for several southern African species; Young (1990) for Columbian ground squirrels, S. columbianus in Alberta; Yensen et al. (1991) for Idaho ground squirrels, S. brunneu in Idaho; Advani and Jain (1982) for the sand colored rat, R. gleadowi in the Indian desert) soil type (Reynolds and Wakkinen (1987); Laundre (1989) and age (Mushinsky and Esman (1994) for G. polyphemus].

Above ground habitat variables may play a role in the individual digger's decision to excavate. These include the spatial arrangement of the burrow entrances (Stromberg (1978) for C. leucurus and C. ludovicianus), distance to resources such as wet areas [Evans (1951) for striped ground squirrels; Gahr (1992) for pygmy rabbits, Brachylagus idahoensis in Washington] or food patches, cover [Young (1990) for S. columbianus in Alberta; Fitch (1948) for S. beecheyi], and the cryptic nature of the burrow opening [Tognelli et al. (1995) for the southern mountain cavy, Microcavia australis in Argentina; Kinlaw (1990) for eastern spotted skunks, Spilogale putorius in xeric scrub of Florida]. In areas where sloped ground is available, some species may seem to prefer it. Zimmerman (1990) reports that nine-banded armadillos, Dasypus novemcinctus in Oklahoma prefer to burrow in sloped areas. In south-central Florida, armadillos will readily burrow in flat terrain (Kinlaw, pers. obs.), as that is primarily what is available.

Functional Ecology, Burrow Architecture, and Burrowing Behavior

The historical view of the function of the burrow is that it represents a micro-refuge, or shelter, from environmental stresses such as temperature extremes, fire or predation (e.g., Burns et al. 1989 for C. leucurus). Only recently have these claims been substantiated by

observational or radio-telemetry studies, modeling, and comparisons of measurements of burrow conditions with those on the surface.

A major problem for vertebrates in desert regions is the high mean diurnal temperature during summer. When the gerbil (Meriones hurrianae) of the Thar desert develops hyperthermia due to continuous exposure to sun, it intermittently visits the cooler environments of the burrow and unloads the excessive heat. This may be the reason that diurnal rodents excavate extensive, multi-tier burrows as compared to the nocturnal rodents (Prakash 1997). Ground squirrels apparently respond to this environmental stress by using shallower burrows for summer retreats and deeper burrows in winter (Bartholomew and Hudson 1961). Convincing data that temperatures in deeper parts of burrows are more moderate below the thermal isocline that marks daily fluctuations in soil temperatures have been reported by van Heerden and Dauth (1987) for the ground squirrel, Xerus inauris in southern Africa, and Kay and Whitford (1978), for banner-tailed kangaroo rats, D. spectabilis in the Chihuahuan desert. When thermoregulatory measurements of a burrow dwelling rodent, Gerbillurus paeba, and a rock crevice dweller, Aethomys namaquensis, were compared, the burrow dweller had a higher rate of conductance to remove metabolic heat produced by the body (Buffenstein 1984), an adaptation for use of the burrow as a heat sink. Instead of a heat sink, sand goannas (Varanus gouldii) in southern Australia use their burrows as a heat trap, by re-entering the burrows in the afternoon when burrow temperatures were still increasing, thus extending the period of elevated body temperatures (King 1980). Desert tortoises (G. agassizii) were reported to use burrows as thermoregulatory devices (Woodbury and Hardy 1948); and they may plug entrances to their burrows to increase this thermoregulatory advantage (Luckenbach 1982).

A second important obstacle to existence in desert and arid regions is the tremendous dehydration effect of the dry desert air on life forms. Burrow micro-climate was much more favorable in kangaroo rat burrows than on the surface, since the relative humidity was near saturation (Kay and Whitford 1978). Similarly, relative humidity in C. leucurus burrows was higher than above ground (Clark 1971). Evaporative water loss for desert tortoises (G. agassizii), predicted using biophysical models, was consistently lower inside burrows than on the surface (Bulova 1994). Laboratory studies using artificial burrows have generally confirmed these temperature and gas findings.

Seasonal fires represent a common environmental assault, and in plant communities that have co-evolved with fire, burrows play a key role in the population dynamics of both burrowers and non-burrowers. In the Australian heath, five species of Pseudomys that burrow commonly survive the acute phase of burns and colonize early successional stages post-fire. After one fire, many carcasses of Antechinus pseudocheirus, a non-burrower were found. The survivors were individuals that took refuge in wombat burrows (Friend 1993). Pre- and post-fire residency (measured by density, sex ratio and age classes) of a key burrower in the western U.S. desert, D. spectabilis were unaffected by fire Levine et al. 1995). Simons (1991) trapped a non-burrower [the white-throated woodrat (Neotoma albigula) and three burrowers: Merriam's kangaroo rat (D. merriami), the Arizona pocket mouse (Perognathus amplus), and Bailey's pocket mouse (Chaetodipus baileyi)] before and after a fire in the Arizona desert. Neotoma occupies houses made of sticks and debris that burn intensely, and survival in and emigration from the burned area greatly decreased, due to direct mortality. Immediate population changes did not occur in the heteromyids due to the fire, but population sizes did change due to the indirect effect of the lack of vegetational

cover in the burned area. The worst environmental extreme imaginable is probably an atomic blast and kangaroo rats have survived this catastrophe at the Nevada test grounds by remaining in their burrows (Anderson and Allred 1964).

The morphology and complexity of the burrow can also serve an anti-predator function. Potential predators can be thwarted by the diameter, depth and length of burrow (Laundre 1989). Complex, anastomosing burrows can confuse a predator hunting through it for the first time (Bronner 1992). Some species, such as the Cape short-eared gerbil (Desmodillus auricularis) and the old field mouse (Peromyscus polionotus) have escape burrows to use as exits. McLean (1978) observed that female Columbian ground squirrel (S. columbianus) dug small, inconspicuous chambers on the periphery of the major burrow system, which they used for parturition. These small holes were plugged; McLean (1978) speculated that the plugs were responses to predation by nonresident conspecific “marauding males.” Black-tailed prairie dogs (C. ludovicianus) deposit burrow diggings into a high mound at the burrow entrance, and use the height of the mound by perching atop the mound to scan the horizon for predators. (King 1959). The value of burrows and natural cavities in Australia was demonstrated by Smith and Quin (1996) where conilurine rodents have suffered a higher rate of extinction and decline than other mammalian taxa; the investigators attributed this to “hyper-predation” by introduced cats, foxes, and dingos. Their survey showed a less severe decline in those conilurines which use burrows and natural cavities.

There is an established literature dealing with food hoarding by animals, including desert rodents (see review by Vander Wall 1990), illustrating that the burrow serves a food storage function. In arid environments, seeds of various Mojave desert plants can absorb up to 25% of their mass in additional water from vapor in high humidities (Morton and

MacMillen 1982) such as found in a mammal burrow. Kangaroo rats can select seeds that yield more metabolic water (Frank 1988a) and preformed water (Frank 1988b, 1988c). Nagy and Gruchacz (1994) reported that seeds of the creosote bush (Larrea tridentata) were a major component of the diet of Merriam's kangaroo rat (D. merriami), an interesting finding, since burrows of this species have been shown to positively influence the growth of creosote (Chew and Whitford 1992), as discussed below.

In species categorized as "primary excavators," the burrow serves as a focal point for their activities. Radio-telemetered D. merriami in the arid Colorado Desert showed a high degree of clustering, which reflected the occupancy of day burrows (Behrends et al. 1985). In the semi-arid scrub of Argentina, radio-telemetered plains vizcachas (L. maximus) had a home range centered around a communal burrow system (Branch 1993.)

That the burrow is a key environmental resource can be appreciated when considering philopatry or dispersal. Natal philopatry (retention of offspring in natal home ranges past the age of independence from parents) might be expected to occur more in primary excavators (who have invested much energy in constructing the resource) than non-digging species, especially if the burrower hoards food in the burrow. Jones (1984) demonstrated this phenomena in D. spectabilis in southeastern Arizona. Pfeifer (1980) showed that the limited availability of suitable maternity burrow sites influences juvenile female dispersal in Wyoming ground squirrels (S. richardsonii). Secure burrows are critical for mammals with altricial young, which are helpless and vulnerable for many weeks.

It is well known that mole crickets (Scapteriscus acletus) and perhaps other burrowing insects use their burrow as an acoustic horn to amplify their calls (Bennet-Clark 1987). The acoustic properties of the burrow of Heleioporus, a burrowing frog from West Australia, were

examined by Bailey and Roberts (1981), who found that the burrow enhanced the principal frequency component of the call by resonance. By using suspended microphones, Randall and Lewis (1997) determined that the sealed burrow of foot-drumming kangaroo rats (D. spectabilis) provides a quiet place to listen for substrate-borne drummings from conspecifics. It is known that gerbils can detect low frequency sound such as footfalls on the soil from underground (Kingdon 1990). Thus, the burrow can serve as a communication device.

From this literature search, I have tabulated nine measured or hypothesized specific functions of burrows. Three of these have survival value: burrows protect from environmental extremes, lessen the risk of predation, and allow access to hoarded food. Burrows are often used as a place to heal from injury or disease; this has obvious survival value; I have categorized this as a “hospital” function. Burrows provide a familiar and safe place for reproduction, a population growth function. The downward allowing more control over it’s micro-environment (a “comfort” function). Species that utilize a burrow built by another enjoy a savings of both energy and time, since they don’t have to invest in the enterprise themselves. Some species not only give birth but rear their young in burrows; thus there is a socialization component to burrow life for these species. Finally, different species have evolved methods to capitalize on the acoustical properties of the burrow chamber for communication.

Hansell (1993) stressed that burrows and nests have potent biological influences on communities and lists them: the reinforcement of social life; the alteration of habitats; the concentration of resources; the exploitation of the resources of others; and the invasion of new habitats. These influences usually benefit the burrower.

Classical Ecological Issues

Three areas of ecology that have a firm conceptual basis are competition theory, foraging theory and island biogeography. Here I briefly describe studies that directly involve the burrow with these three classical issues.

In arid areas a recurring question is “ Why are there so many desert rodent species?” Schropfer and Klenn-Fringes (1991) observed that J. jaculus , a bipedal rodent, is less dependent on it's burrow, and uses a wide foraging area in which it finds new food patches frequently. By following this foraging mode, this species only used a small part of the overall resource. They observed that G. gerbillus, a quadrupedal rodent, stays close to the burrow, intensively using the area around the burrow, perhaps utilizing close to 100% of the food resource. Their hypothesis is that competition for food is the key, and this extent of this competition is related to the way the burrow is used, in particular the foraging distance from the burrow. Similarly, Bowers and Brown (1992) asked if the proximity of burrows of a dominant species, D. spectabilis, affected spatial usage patterns of other rodents in the community. They found that captures of five other species did increase with distance away from D. spectabilis mounds. This data is at least congruent with that of Schropfer and Klenn-Fringes (1991) and underscores the importance of the burrow in the community. Regarding competition for space, Layne and Jackson (1994) using radiotelemetry methodology in south Florida, showed that the cotton mouse (P. gossypinus) occupies the main tunnel of gopher tortoise burrows, where Florida mice, Podomys floridanus utilize the inside passages of the same burrow system.

Regarding foraging in arid areas where trees are sparse, ground burrowers hold an advantage over arboreal cavity requiring species. If the burrow is damaged, they can simply

re-excavate near the same food patch. However, if the tree (containing a necessary cavity) is destroyed, the arboreal species will usually need to re-locate to a new position, which would probably be further from a food patch. If the food supply shifts, the burrower can simply follow it, and construct an energy-savings refuge near it. For example, radiotracked D. merriami maintained stable core loci centered around day burrows, but moved to new day burrows once every 4 days (Behrends et al. 1985). A novel rotational use of burrow systems has co-evolved in southern Africa. Meerkats (Suricata suricata), yellow mongooses (Cynictis penicillata) and a ground squirrel (X. inauris) alternately use each other's burrow system as they move about following shifting food resources (Lynch 1980). The proximity of a burrow near an extensive food resource also means that the forager can afford to reduce activity during inclement weather conditions. Van Aarde et al. (1992) used this hypothesis to explain why radio-tracked aardvark (O. afer) reduced foraging activity during cold, dry months in southern Africa.

Vigilance behavior is related to the distance of the forager from the burrow. Holmes (1984) observed foraging hoary marmots (Marmota caligata) looking up more with increasing distance from the burrow, and Frase and Armitage (1984) observed yellow-bellied marmots (M. flaviventris) foraging closer to the home burrow or refuge burrows than further away. Columbian ground squirrel (S. columbianus) feed at a quicker rate with increasing distance from their burrow (Andrusiak and Harestad 1987).

Some burrowing Heteromyidae in arid regions frequently cache food in the burrows, as do some Cricetidae; diagrams and descriptions can be found in Vander Wall (1990). Ellison (1993) dug up burrows of the pouched mouse (Saccostomus campestris) at four localities in South Africa and provides a detailed list of the contents of the cache. For the

scatter hoarding D. merriami, distance from the burrow was a determinant of where food was initially deposited (Daly et al. 1991).

Since colonization and extinction of micro-communities in these open burrow systems can probably be observed and measured easier than in closed systems (e.g., pocket gopher or mole tunnels), some aspects of island biogeography theory can be tested. Distance from a con-specific's burrow was important in colonizing new sites. Using radiotelemetry, Waddell (1986) found that dispersing S. columbianus did not colonize patches of suitable habitat, but rather settled near other squirrels (e.g., burrow systems). The importance of the burrows for colonization was demonstrated by Apa et al. (1990), who removed 45% of a C. ludovicianus colony by applying rodenticide; the site was re-colonized within 10 months. The importance of site fidelity was further underscored by Salmon et al. (1987) who completely trapped out a S. beecheyi colony and physically destroyed the burrows on a treatment plot, but left intact a control plot. Fifty per cent of the squirrel re-colonized the treatment plot in 5 months (represented 50% of the original population). Interestingly, the burrows were dug in exactly the same location on the treatment plot as they occurred before being destroyed.

Re-colonization is related to prior use. Burrow use patterns may be influenced by chemical cues left by previous inhabitants. Male desert tortoises (G. agassizii) were more likely to use burrows treated with another male's chin gland secretion rather than control burrows; females were less likely to use burrows treated with feces from another female than controls burrows during the nesting season (Bulova 1994).

Animals as Engineers and Resulting Impacts

It is the lack of trees or other vegetative features which could be used as shelter in desert or arid regions that underscore the survival value of underground burrows to the faunal

community. In these harsh regions primary excavators are *prima facie* examples of allogenic ecosystem engineers (Jones et al. 1994) that augment the meager shelter options available for vertebrates in arid environments by providing abiotically moderate physical structures. The availability of these energy saving enclaves across the landscape allow numerous desert species to better optimize their time and energy budgets than if this shelter were not there.

The cumulative effect of these burrow systems depends on the magnitude of six factors (modified from Jones et al. 1994): number of burrows dug in lifetime; density of burrows in the area; spatial distribution of burrows; Length of time species present in area; Durability of burrow in absence of original engineer; and number and types of resource flows that are modulated by burrows. The durability of a burrow may relate to: the type of mechanical motion used to dig; the angle at which it was dug, which is a function of the mechanical digging motion of the excavator, and the substrate. Many mammals dig burrows using a ventro-posterior motion with their paws (from front to rear), and push the soil out with their hind feet. The resulting burrows often are simply hollowed out tunnels. Gopher tortoises, on the other hand, dig with a sideways motion, and in doing so compact the soil laterally (Wilson et al. 1991); additionally, the carapace probably exerts some pressure on the roof of the tunnel. The resulting tunnel has somewhat hardened walls; this may play a role in preventing seepage of water into the tunnel, in pulverization of the excavated soil, and in preserving the tunnel over time (Wilson et al. 1991). A second variable affecting the age of the burrow is the angle of repose, the steepest angle at which a substrate will remain cohesive before particles will tumble down due to gravity (Polis 1986). If the tunnel opening drops at a steep vertical angle, it is more likely to fill up with wind-blown soil, debris, or rain-wash. Some excavators avoid tunnel collapse by digging under roots of trees or shrubs, which

act to physically support and hold the soil above and around the tunnel. This has been reported in most arid regions [Kowalski and Rzebik-Kowalska (1991) for M. libycus in Algeria; Smithers (1971) for Tatera leucogaster in Botswana; Watts (1995) for P. australis in Australia; Gordon et al. (1985) for Lasiorhinus krefftii in Australia]. The optimal burrow angle in terms of energetic expenditure would be perpendicular to the horizontal (Polis 1986) and desert tortoises will dig directly into the side of a wash (Luckenbach 1982) and gopher tortoises will dig into road banks (pers. obs) if these features are available. Gopherus is constrained to dig with a sideways swimming motion, resulting in a tunnel that enters the surface at a shallower angle than those dug by mammals which can dig with a downward motion with their forepaws.

When these “shelter hot spots” have a high spatial density across the landscape, the primary excavator meets the criteria of Power et al. (1996) as a keystone species, because the variety of impacts of burrowers in arid ecosystems makes their importance disproportionate to their abundance. After reviewing impacts of burrowing by G. polyphemus on xeromorphic shrub occurring on ridges of sandy soil in Florida, Eisenberg (1983) classified this primary excavator as a keystone species. Burrowers in arid regions clearly modify habitats and abiotic factors, and should be referred to as “keystone modifiers” (Mills et al. 1993). A multi-taxonomic group of vertebrate burrowers that have existed in an area over evolutionary time should be considered a keystone guild because of the cumulative effects of these burrow systems in structuring the faunal community, affecting soil nutrient cycles, impacting plant diversity and succession, and causing major geomorphic changes.

In the sections that follow, I view the burrowing phenomena as an ecosystem process and I examine the impacts of this process from the standpoint of the following traditional

disciplines: geomorphology; soil dynamics; plant ecology, animal community ecology; and landscape ecology. An advantage in using this over-simplified and artificial approach is that it allow natural resource scientists an introduction into this ecological phenomena from their own professional orientation.

Geomorphology

Using data from various workers on burrows dug in Florida's xeric scrubland soil Butler (1995) generalized that this reptile can excavate 40-100 m³ of sediment per hectare. Butler (1995) also extrapolated from data by Kolb (1991, 1994) on European rabbits (*O. cuniculus*) and derived a figure ranging from 2 to 63 m³ per hectare of sediment displaced. Although Kolb's data were from England, similar magnitudes of soil displacement might apply in arid regions of Australia, where they have been introduced. The geomorphic effect may depend on whether the soil had been previously disturbed or loosened. Ground squirrels (*S. townsendii*) and Ord's kangaroo rats (*D. ordii*) both excavated relatively more soil from below 50 cm in disturbed than undisturbed soils (Reynolds and Laundre 1988). Koford (1958) calculated that 12 prairie dog burrows have a volume of 2.7 m³ and represent the removal of 3.63 metric tons of soil to the surface. However an additional consideration is the effect of secondary modifiers or predators, especially badgers. Campbell and Clark (1981) reported that 10-27% of the burrows on the sites they studied had been enlarged by badgers in pursuit of prairie dogs.

In the semiarid regions of Australia, hairy-nosed wombats (*Lasiorhinus latifrons*) can burrow through compact soil as well as thick layers of calcrete. The mound created by the tailings can rise 1 m. above the surrounding topography (Loffler and Margules 1980), and large circular areas of bare ground surrounding the burrow opening are created. Although

geomorphologic data are not available, Butler (1995) reports that wombats are capable of landform creation and massive sediment displacement. The landscape level effects of wombats are visible from satellite photographs, as are landforms created by viscachas burrows in arid regions of Argentina (Branch et al. 1996).

After surveying all major phyla of animals that burrow, Butler (1995) recognized that “although an individual species or genus may not have geographically widespread geomorphic influence, it may have profound effects locally;” and “the geomorphic effects of animals must be considered collectively in order truly to be appreciated.”

Hydrology is clearly altered by the burrows. In the cool desert of Idaho, Laundre (1993) compared the amount of water added to the soil profile from spring snowmelt recharge in areas subject to ground squirrel burrowing to that in nearby areas without burrows. He found that recharge amounts in areas with burrows were significantly higher than in nonburrow areas. He found that 21% more of the winter precipitation infiltrated into the soil near burrows, and the amount was positively related to burrow density, allowing vertical penetration of the water to deeper portions of the soil profile than in nonburrow areas.

Pedological Effects of Burrowing on the Soil

In many environments, burrowing has been shown to affect soil texture and structure, fertility, infiltration, soil mixing, inorganic distribution, mineralization rates, and surface runoff (see reviews by Reichman and Smith 1990, Meadows and Meadows 1992, Butler 1995). A major burrower in semi-arid regions of North America, the black-tailed prairie dogs (*Cynomys ludovicianus*) has been reported to add organic matter and nutrient salts to the soil, improve the soil structure, and increase water infiltration (Koford 1958); enrichment of phosphorus by prairie dogs was reported by Carlson and White (1988). In desert regions,

soils are low in nitrogen and phosphorus (Louw and Seely 1982), and the concentration of nitrogen-rich feces in and around burrow openings may raise the local nutrient status (Dean and Milton 1991).

Pedological Effects of the Soil Type on Burrow Architecture and Species Distribution

For vertebrates, burrow structure varies among and within species, and this variation may be related to physical properties of soil (Anderson and Allred 1964, Reynolds and Wakkinen 1987, Reichman and Smith 1990). The geographic distribution of some burrowing mammals has been related to edaphic factors. Soil structure variables were the main factors affecting distribution of Wagner's gerbil (G. dasyurus) in Israel; the preference was for loess mixed with rocks, which permitted easy digging (Shenbrot et al. 1997). Weiss and Verts (1984) found more pygmy rabbits burrow entrances at sites where soils were significantly deeper and looser than at adjacent sites in Oregon. The complexity or tortuosity of burrows has been shown to be related to the clay and silt content for two rodents, but not a third (Laundre and Reynolds 1993, Figure 2-1). Feldhamer (1979) found a direct correlation between density of pocket mice (P. parvus) and the percentage of sand, and an inverse relationship with the percentage of clay. In that xeric shrub community, chipmunk (Tamias minimus) density was directly related to percentage of clay in soil, and Feldhamer (1979) suggested that chipmunks did not find it as difficult as the smaller pocket mice to dig through a sometimes hard, consolidated soil surface of high clay fraction. Moreover, a species may alter or eliminate its burrowing activities in unsuitable soils. Hispid cotton rats (Sigmodon hispidus) had seven times more burrows systems in Florida on a sandy substrate (Pomello series) than in Kansas on a compact clay humus Oska series soil (Shump 1976).

Vegetation Effects

Burrowing species have been shown to have a variety of effects on arid plant communities. A common finding is that patches are created which promote growth of annuals. A burrowing rodent in arid grassy South African dunefields, T. brandtsii, maintained circles of bare ground around its warren, creating spaces for annual plants to germinate and grow (Dean and Milton 1991). Similar findings have been reported for vizcachas, L. maximus in semi-arid scrub in Argentina (Branch et al. 1999), kangaroo rats, D. spectabilis, in the Chihuahuan desert [Moroka et al. (1982); Brown and Heske (1990); Guo (1996)], and prairie dogs, Cynomys ludovicianus, in semi-arid regions of the western United States (Whicker and Detline 1988). Arctic ground squirrels, (S. parryii), were reported to increase the floristic diversity on sand and gravel eskers of non-alpine arctic tundra (Mallory and Heffernan 1987). A different vegetative composition was found on excavated badger (Taxidea taxus) burrow mounds in semi-arid regions of the United States (Gibson 1989), and more pioneer species on gopher tortoise (G. polyphemus) mounds on sandhills in Florida (Kaczor and Hartnett 1990). Since biodiversity is maintained if soil disturbances are small (Futuyma 1994), the array of small patches created by animal burrows across the landscape should occur at the appropriate scale to stimulate local floristic changes.

Animal Community Ecology

Physical structure can interact with ecological processes in varied and complex ways, and influence how communities assemble, function, and persist (Bell et al. 1991). One of the prime engineering structures that animals build are artifacts that provide shelter for other animals, such as tree cavities, ground burrows, etc. Examples from the literature that report

the diversity of species occurring in different sized ground burrows are presented in Table 2-1.

Ceballos and Pacheco (1999) reported increased species richness of small mammals in prairie dog colonies compared to grasslands without prairie dogs. After open burrows are first dug, they often have a successional sequence of faunal invasion and colonization.

Different species may occupy the burrows for a variety of reasons; the size of the opening appears to be important in burrow selection (Speake 1981). Taxa that have a co-evolutionary history together may develop patterns of burrow-sharing, ranging from commensalism to obligatory relationships as in the example of the fringe-toed lizard (Uma exsul) given earlier. This is consistent with Allen and Hoekstra's (1992) view that composition of an animal community is not a happenstance collection but the difference in the organisms because the other community members can be expected to be present. Thus, different species might accommodate each other in various ways in the burrow. Burrows dug by these "keystone" habitat modifiers (Mills et al. 1993) can be critically important for many species in the ecosystem. In fact, early Russian biologists (e.g., Vlasov 1937) gave the burrow "biotope" status. Hawkins and Nicoletto (1992) concluded that the burrows of banner-tailed kangaroo rats (D. spectabilis) can structure the spatial organization of animal communities in the arid grasslands of New Mexico, by providing habitat patches that are abiotically moderate and which contain high concentrations of food resources.

In addition to the energetic requirement of constantly maintaining the burrow, there are disadvantages to this mode of existence. Seasonal flooding of burrows has been demonstrated to cause mortality to the fringe-tailed gerbil (T. robusta, Senzota 1984) and anecdotally linked to decreases in springhare (Pedetes capensis) numbers in southern Africa

(Lynch 1983). Invasive species that burrow, such as the imported fire ant (Solenopsis invicta), were documented to have a negative relationship with the northern pygmy mouse (Baiomys taylori, Killion et al. 1995).

Future Research and a Conceptual Model

Open burrow systems are more than just “holes in the ground”; they are an important resource for many species. They represent a tractable system for ecological experimentation. There are fundamental differences in availability and ease of preparation between ground burrows and tree cavities, and this difference may have implications regarding foraging, spacing, and social structure for species that construct each respective resource. There are also differences between “open” and “closed” ground burrows, with the former perhaps being more amenable to island biogeographical studies. Questions dealing with the division and use of space by the same or different species within the close confines of the burrow can be addressed. Since the animal is the “sculptor” and the soil is his medium, incredibly complex designs can be carved out. Faunal diversity may vary with geometry of the burrow. Some species constantly modify their burrow, adding complexity over time; in arid environments where burrow shape can remain intact over long periods of time, I suggest that natural selection will favor this additional spatial resource. What is the relative importance of burrowing as opposed to other types of “ecosystem engineering” (Jones et al. 1994) in arid zones? Furthermore, there may be principles hidden away in the fields of architectural theory, civil engineering, soil mechanics or soil physics, which may be related to acoustics or longevity of the burrow, when different shapes or designs are compared. Are there major patterns in distribution and abundance of organisms that can be explained by this form of ecosystem engineering (Jones et al. 1994)?

A long term study in Arizona (Chew and Whitford 1992) demonstrated an unusual positive impact of mounds of the kangaroo rat on the survival of creosote bush (L. tridentata). Similar long term studies are needed to investigate whether the distribution of plants in arid regions is partly comprised of species which germinated from seeds that were cached in rodent burrows, in view of Naumov and Lobachev's (1975) observation that much of the food of tamarisk gerbils (M. tamariscinus) and mid-day gerbils (M. meridianus) store in the wild often is left unused.

Here I have listed some crude similarities in burrowing behavior between endotherms and ectotherms on different continents and the resulting impacts of this burrowing. Are there some central principles of this ecological phenomena between taxa and between habitats, and at different scales? Are there "assembly rules" of community structure in the micro-communities inhabiting ground burrows, similar to macro-communities (e.g., Diamond 1975).

Because of the combined effect of open burrow systems on geomorphology, plant communities and faunal diversity, I suggest that these systems have "emergent properties"; that is, landscape level effects, illustrated in the following conceptual model (Figure 2-2). Cellular automata models perhaps could be one approach to model the large scale patterns that ultimately result from this "profound local effect."

Table 2-1. Diversity of animal fauna found in burrows in semi-arid environments or environments with dry, sandy soils.

Type of Burrow	Diversity	Locality	Reference
Gopher Tortoise	302 invertebrates 60 vertebrates	Florida, USA	Jackson and Milstrey, 1989
Desert tortoise	8 invertebrates, 12 reptiles	California, USA	Luckenbach, 1982
Kangaroo rat	2 birds, 9 mammals 14 species of reptiles, 22 families of insects, 6 orders of non-insect arthropods	New Mexico, USA	Hawkins and Nicoletto, 1992
Aardvark	20 species of vertebrates	Southern Africa	Smithers, 1971
Springhare	7 species of vertebrates	Southern Africa	Smithers, 1971
Black-tailed prairie dog	82 species of invertebrates	Oklahoma, USA	Wilcomb, 1954

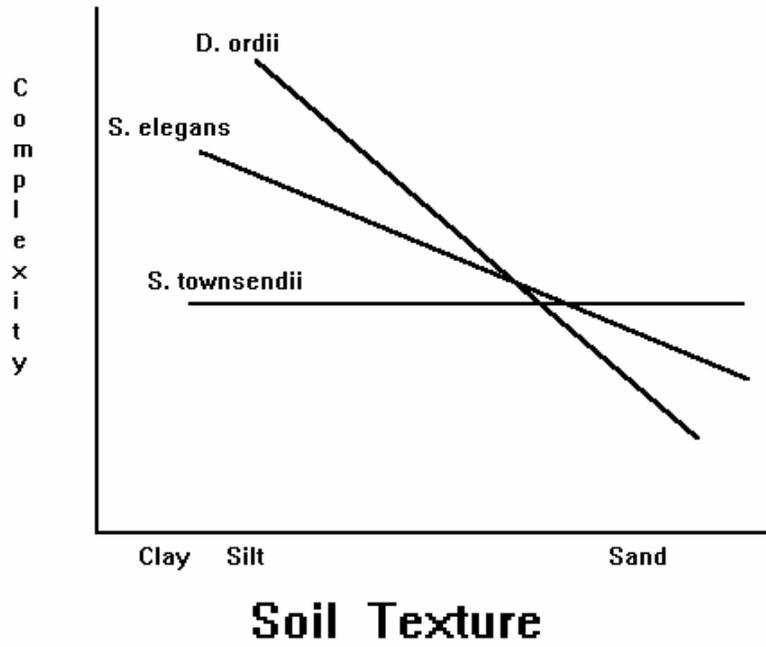


Figure 2-1. Complexity of burrows dug by three rodents in soils with varying soil textures. Modified from Laundre and Reynolds (1993).

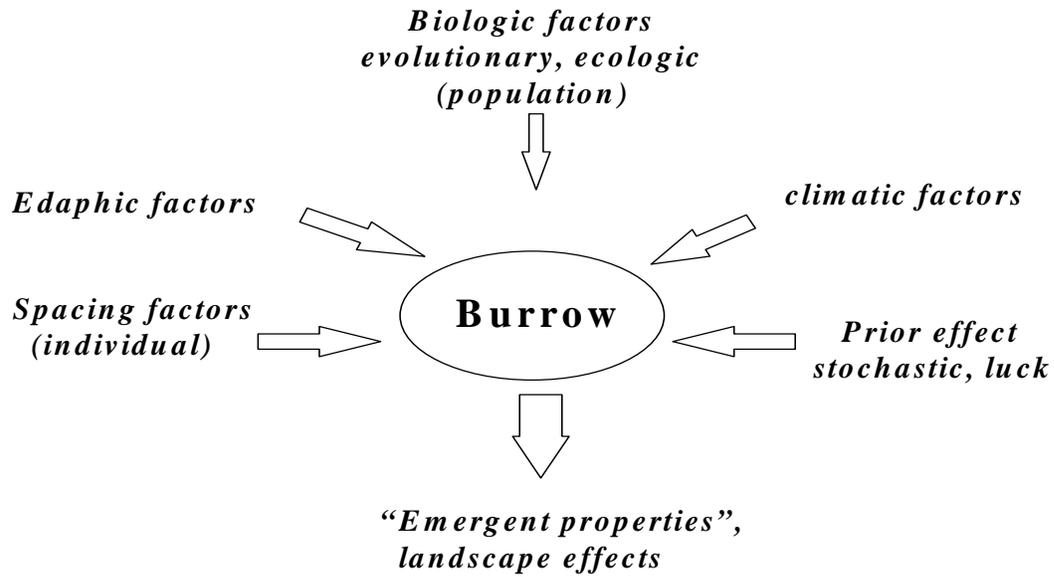


Figure 2-2. Conceptual model of landscape-level effects of burrow systems.

CHAPTER 3
SAMPLING APPROACHES TO ESTIMATE DENSITY OF
GOPHER TORTOISES (Gopherus polyphemus)
IN CENTRAL FLORIDA

Limitations of Current Gopher Tortoise Burrow Census Methods

Florida has a system of ancient shorelines, some dating as far back as the Pliocene, which run down the middle of the peninsula (White 1970). These relic dune ridges of deep, well drained sand support a fire-adapted, xeric plant community classified as “scrub”. Scrub usually exists as irregularly shaped patches called “scrub islands”, part of a mosaic of xeric and mesic communities, separated vertically and horizontally by only a few meters. On these ridge “hilltops”, an estimated 200 ancient scrub islands have been identified (Christman and Judd 1990); between 40-60% of scrub species are considered to be endemic (Myers 1990). Scrub is frequently cited as Florida’s most distinct ecosystem and scrub fauna represent one of the most endangered upland systems of the world.

An integral part of scrub and similar upland communities that grow on sandy soil is the gopher tortoise (Gopherus polyphemus), a large fossorial chelonian that constructs extensive underground burrows (Figure 3-1). The ICUN (1996) considers the species “vulnerable” to extinction, and it currently is under consideration for reclassification by the Florida Fish and Wildlife Commission (2006a) as a threatened species in the state. Moreover, the Commission is strengthening protection of its burrows (FWC 2006b). Because Gopherus burrows serve as refugia for many species, the gopher tortoise has been referred to as a keystone species (Eisenberg 1983). Two threatened vertebrates, the gopher frog (Rana capito aesopus) and the Florida Mouse (Podomys floridanus) are greatly dependent on the tortoise burrows for refugia (Godley 1992, Layne 1992), and a loss of the burrows due to

dwindling populations of the tortoise would negatively impact the tenuous existence of these species also.

The rapid urbanization of Florida has caused a tremendous decline in the upland habitats favored by the tortoise, and future intact populations will probably only survive in protected areas. Because military bases in the southeastern United States are usually closed to the public and the vegetative communities are subject to occasional wildfires due to the use of live ordnance, they serve as *de facto* reserves for this fire-adapted species.

Visual counts of tortoises cannot be used as a census technique, because individuals remain in underground burrows much of the time. Since burrows play a major role in the functional ecology of this species (used for thermal protection (Douglass and Layne 1978), predator avoidance, and protection from periodic fires), burrow counts have been used to estimate number of tortoises. Auffenberg and Franz (1982) used burrow counts on strip transects 150 m long by 7 m wide; however, the most commonly used size is 250 x 20 m, following Cox et al. (1987). With this method the population estimate of tortoises is determined by multiplying the occupancy rate (percentage of burrows with an individual tortoise in residence) by the number of burrows counted in a known area. This “correction factor” varies in different parts of the species’ range and if applied should be site-specific (Burke, 1989; Witz et al. 1992; McCoy and Mushinsky 1992). The Cox et al. (1987) method was originally devised to be used at sites scheduled to be developed, where visibility is often moderate to good; if visibility is low due to thick vegetation, they briefly recommend line transect sampling (Burnham et al. 1980).

Line transect sampling, now called distance sampling (Buckland et al. 1993; Buckland et al. 2001; Buckland et al. 2004) has excellent theoretical underpinnings and is the best

method to use in field situations where its assumptions are met. This method allows for missed burrows by calculating a detection function, which is used to determine the total number of objects (number detected plus number not detected) in the sampled area. The key assumptions are that objects on the survey line are detected with certainty and the detection function is “shoulder” shaped, indicating a high detection probability (e.g., good visibility if visual objects are to be detected). However, if these two assumptions are not met, the reliability of this technique is poor (Buckland et al. 1993). Field results are not always consistent with this method; Epperson (1997) found surprising variability between 3 trained observers using line transect sampling for tortoise burrows

Additionally, if the objects of interest occur in a systematic pattern, distance methods can yield highly biased results if the field surveyor is unaware of the pattern and chooses his transect direction along the pattern. The software program DISTANCE was developed for use with distance sampling, and requires a minimum sample size of about 60-80 (Buckland et al. 1993).

In a preliminary survey I conducted of tortoise burrows at Avon Park Air Force Range (APR) involving 148 line transects totaling over 101 km, the criteria needed to implement distance sampling could not be met (Kinlaw, unpublished data). That survey was based on vegetation types, and not enough burrows were located in each type to meet the minimum sample size requirements of the program. Due to the low visibility caused by the thick vegetation, detectability dropped off dramatically. Moreover, in many of these irregularly shaped or small scrub patches, my transect lines intersected either “edge” or completely different vegetation types, which would have confounded a vegetation-based analysis.

While attempting to census tortoise burrows using linear strips at Kennedy Space Center, FL (KSC), Breininger (pers. comm., February 16, 2006, Dynamac Corporation, KSC, FL) recognized a systematic pattern in which the burrows were more concentrated along the edges of linear strips of elevated terraces which are oriented in a north-south direction. Because the lower areas between the terraces are usually flooded, by necessity the surveyor's transects needed to follow the terraces. Those transects that followed the systematic pattern of the burrows would have introduced bias into his estimates. Breininger's solution was to switch methods, and he began to use burrow counts on 30 x 50 m randomly selected quadrats (Breininger et al. 1988). I encountered a similar systematic pattern of burrows at some APR sites, and realized that at hilly, undulating terrains in Florida's landscape where tortoises occur, such a burrow pattern would not be unexpected. Moreover, in a review of methods used to census tortoise burrows, Carthy et al. (2005) concluded that quadrat sampling was a "default" technique that offered advantages over line transect methods.

Since my pilot study showed that distance sampling would be difficult to implement at APR, I switched to quadrat sampling, using 1 hectare plots. This size was chosen based on the reported home range of 0.5 ha (McRae et al. 1981) under the working assumption that this was probably the largest size that would capture an adequate number of burrows, yet could still be surveyed in a time-efficient manner. This study presents a standardized protocol using one hectare sized plots, as a compromise between precision, logistics, and biology, when the biologist feels that quadrat sampling is the appropriate method for sampling tortoise burrows. The method uses "nearly complete" counts on plots and includes simulation to assess the small amount of bias induced by under- or overcounting burrows.

There were three questions that prompted this research. First, do tortoises dig more burrows in some habitats than others? Secondly, what is the population size of tortoises in the habitat with the highest density of burrows? Thirdly, because counts of biological features often fit the negative binomial distribution (NBD; Bliss 1953), does the burrow data fit this or some other statistical model for each sampled habitats?

Materials and Methods

Avon Park Air Force Range (APR) is a 42,927 hectare military reservation located in Polk and Highlands counties, Florida. The major topographic feature is a north to south trending, sand ridge, 53.3 m. above sea level at the highest point, part of Florida's relic system of dune ridges (Figure 3-2). At APR, oak scrub and sand pine scrub occur in irregularly shaped patches. Florida oak scrub vegetation is a xeromorphic shrub community dominated by a layer of evergreen oaks (Quercus geminata, Q. myrtifolia, Q. inopine, Q. chapmanii) and often Florida rosemary (Ceratiola ericoides); if an overstory of sand pine (Pinus clausa) exists, it is referred to as sand pine scrub (Myers 1990). Gopher tortoises occupy the scrub vegetation that occurs along the ridge, but also occur in sporadic patches of deeper sand found at lower elevations. The primary soil type in these scrub areas is Myakka fine sand (Ford et al. 1990). Areas of oak hammock occur usually as irregularly shaped strips along the Kissimmee River or Lake Arbuckle. The soil maps indicate that this vegetation type occurs on Myakka fine sand and Bassinger sand. The sand pine scrub stands occurred on either Archbold sand or Duette sand. The slash pine (Pinus elliottii) communities occur throughout APR on a variety of soil types.

To survey the burrows, I followed a stratified random sampling design. From a GIS map of the plant communities of APR, I selected plots in each of the four upland

communities and each habitat type was gridded off into 1- hectare plots (Figure 4-3). Fifty five oak scrub plots, 53 pine community plots, 23 sand pine plots, and 17 oak hammock plots were randomly selected using a random numbers table (Steel and Torrie 1980) and subsequently surveyed. Proportional sampling effort was increased in the preferred oak scrub habitat, but reduced in mesic oak hammock and overgrown sand pine habitats, because tortoises will avoid those habitats (Auffenberg and Iverson 1979). My “pine” category included the following categories of the Florida Natural Area Inventory (FNAI, 2004): mesic flatwoods, scrubby flatwoods, and wet flatwoods.

The theoretical model I used to estimate the total number of burrows in each habitat was the canonical estimator of Williams et al. (2001), which is based on count statistics:

$$\hat{N}_{\text{burrows}} = C / \alpha\beta$$

where \hat{N} = population estimate of burrows,
 C = count of burrows,
 α = fraction of the total area sampled,
and β = detection probability

This estimator is unbiased if α and β are unbiased (Williams et al. 2001). For each of the 4 habitats, α was determined from the GIS maps and equaled 0.031, 0.044, 0.019, and 0.002, for oak scrub, sand pine, oak hammock, and pine flatwoods, respectively. If β equals unity, the above estimator reduces to a simple random sample estimator.

A key source of model bias in animal population estimation is unrecognized or disregarded detection probability (Williams et al. 2001). Bias can occur in surveys such as this if the surveyor assumes all burrows were sighted ($\beta = 1$) when they were not (non-response error, Thompson et al. 1998). To avoid this problem, each plot was clearly marked with identifying markers and one, two, or occasionally three surveyors then followed a

standardized procedure and slowly paced out 10 parallel transects, 10 meters apart, usually in a N-S or E-W cardinal direction. To avoid bias due to mis-classification of burrows (response error, Thompson et al. 1998), surveyors were trained carefully, with verbal and written instructions, on burrow classification. Because of these intense efforts to carefully mark boundaries and thoroughly search each plot, I assumed a β as one. Due to high variability and low sample size in two of the habitats, the usual variance estimators could not be used. Therefore, I constructed 95% confidence intervals around the mean empirically by using the accelerated bias-corrected percentile method (Efron and Tibshirani 1986, Manly 1997).

To determine the occupancy rate of tortoises using the burrows in the scrub, the survey team used a video-probe camera to visually examine the inside of randomly selected burrows during the winter, 1997. Observations in which the camera operator was unable to move the camera completely to the end of the burrow were discarded. I again used the accelerated bias-adjusted percentile method (Efron and Tibshirani 1986) to calculate a confidence interval for the occupancy rate based on the distribution of replicate bootstrapped samples.

To determine if there was a habitat effect, I tested the null hypothesis that habitat and burrow count were not associated versus the alternative that there was an association between these variables.

Since the burrow density at APR appeared to be lower than that of other sites in Florida, I was curious to see if the burrows were dug in a random fashion or were aggregated. Since a preliminary graph of the burrow counts resembled a negative binomial distribution for all four habitats (oak scrub illustrated in Figure 3-4), I began by formally testing the

dataset for each habitat with the null hypothesis of a random or Poisson distribution versus the alternative that the distribution showed some clumped pattern, such as the negative binomial. A variance-mean ratio test for clumped distributions was used for the pine, oak hammock, and sand pine datasets; a chi-squared test was used for the oak scrub dataset. I used Green's index (Green 1966) to quantify any aggregation, because it is independent of density and sample size (Malhado and Petrere 2004, Myers 1978).

I tested for equality among the datasets for each of the four habitats, following the procedure first described by White and Eberhardt (1980). Since the negative binomial can have different means (m) or different exponents (k), there were 4 possible outcomes : 1) all populations differ in mean and k (model $\{k_v, m_v\}$); 2) populations have common k but different means (model $\{k, m_v\}$); 3) populations have common mean but different k (model $\{k_v, m\}$); and 4) all populations the same mean and k (model $\{k, m\}$) (White and Eberhardt 1980). First, I tested goodness of fit to an unconstrained model (i.e. both m and k allowed to vary, model $\{k_v, m_v\}$) of the negative binomial distribution; the null hypothesis was that the data fit this distribution. A likelihood ratio procedure was then used to determine if there were differences in m , k , or both, for alpha = 0.05. Goodness of fit between the observed data and the values expected from a NBD for each of the 4 models was measured using the log-likelihood G statistic (Sokal and Rohlf 1981) and the Akaike Information Criteria (AIC, Anderson et al. 1994).

Using the random number generator function and the optimization function ("Solver") in Microsoft Excel (Fylstra et al. 1998), combined with the Resampling Stats computer program (Blank et al. 2001), I conducted a small simulation study to examine the bias of population estimates of the same magnitude as the scrub estimates under two scenarios which

might occur under field conditions. In scenario 1, I simulated the effects of an undercount of burrows if the surveyors only detected 90%, 80%, 70%, or 60% of the true number of burrows, due to poor visibility from the vegetation, foggy weather, or fatigue. In scenario 2, I examined the impact on my estimates if the multiple surveyors double-counted burrows, resulting in 110%, 120%, 130% or 140% of the actual field count, resulting in an overestimate of abundance. In both scenarios, I “reshuffled” the count data in the Excel spreadsheet using ReSampling Stats, and then forced the constraint (of over-count or undercount) on the resulting column of numbers using the “Solver” routine to obtain a simulated count of burrows for the 55 plots. This value was then extrapolated to all 1762 oak scrub plots. Bias was determined by comparing this simulated population size to the population size extrapolated from the field data. To better understand the effects that aggregation of the burrows might have had on my single sample of 55 plots in oak scrub (scenario 3), it was necessary to keep the total number of burrows sampled constant, but vary the dispersion of burrows in our simulated landscape. I used Green’s Index (GI, Green 1966) of clumping ($\text{variance} - 1/n - 1$) as the dispersion metric and procedurally used the optimization program in Solver as the mechanism to produce each value of GI. First, I resampled our field data (55 plots) 1000 times, and recorded the actual range of GI values we could expect in our empirical “real” population, assuming that the .025 and 0.975 percentile values encompassed the true dispersion that likely occurred in the field. I examined the effects on precision for the following series of GI values: 0.005, 0.010, 0.015, 0.020, 0.025, 0.030, and 0.035, with the following constraints: 1) a constant sampling value of 81; 2) the GI value under consideration was held constant 3) only positive integers that were within the field data values were used.

Results

The null hypothesis that habitat and burrow count were not associated was rejected (Pearson's chi square statistic 19.84, exact p-value 0.0001, StatXact 3.02), indicating a habitat effect. The survey showed that tortoises were found in most of the upland plant communities, but were more concentrated in the oak scrub patches. The mean number of burrows/quadrat in oak scrub was more than triple the density of the other habitats (Table 3-1). Oak scrub also had the highest proportion of plots with active burrows (Table 3-1) and most of the scrub patches we surveyed in the northern half of this military installation had burrows. The variance/mean ratio test rejected a random distribution of burrows in the oak scrub (Chi square statistic = 126.487, 54 df, p-value = 0.000), and a chi-square test did not reject a null hypothesis that a negative binomial distribution fit the data (p-value= 0.2901, alpha=0.05). The odds of encountering a burrow in oak scrub was 4 times or greater than the odds of finding a burrow on any random plot in the other 3 habitats.

Sand pine had the lowest mean density of burrows and the lower 95% confidence level was close to zero (Table 3-1). The survey found the highest probability of not finding a burrow in this habitat. Green's Index (- 0.006) was near zero and the variance/mean ratio (0.862) near unity, both suggestive of a random distribution.

Only about a quarter of the pine plots contained burrows (Table 3-1). Both the variance/mean ratio test (p-value = 0.002) and the G test (Williams 1976) on the frequency distribution of plots (with zero, one, two, etc burrows) indicated that burrows in pine were clumped (G statistic 18.849, 1 df, Quadrat Sampling program, Krebs 1999). However, field observations and the low value of Green's Index (0.029) suggested that this clumping occurred at a low level.

One recently burned oak hammock plot had a cluster of five burrows, resulting in the high index of dispersion (Table 3-1), but 14 of the 16 other oak hammock plots had no burrows. Variance/mean ratio tests rejected a random distribution of the burrows in oak hammock (p-value = 0.000).

There was a small overlap between confidence intervals for the re-sampled data for sand pine and pine, and for pine and oak hammock, indicating that there may not be differences in burrow count between these habitats. There was a considerable overlap between oak hammock and oak scrub.

The results of the LRT tests suggest that model $\{k, m_v\}$ (i.e., k is constant but m differs) is better suited than the other models (Table 3-2). The rejection of reduced model $\{k, m\}$ over $\{k, m_v\}$ was highly significant, as was the rejection of $\{k_v, m\}$ over $(\{k_v, m_v\})$, indicating that m differs. The results for the clumping statistic k were somewhat ambiguous. Model $\{k_v, m\}$ was rejected over $\{k, m\}$, indicating an effect from k , yet model $\{k, m_v\}$ was not rejected over the full model $(\{k_v, m_v\})$ suggesting that the effect from k may not be important. My selection of model $\{k, m_v\}$ as the correct model is supported by the fact that this model had the lowest AIC score (338.779) of the four models (Table 3-2).

Camera scans of 21 out of 36 scrub burrows were judged acceptable. Of these 21 burrows, 12 live tortoises were observed and two burrows had recent tortoise tracks leading into the burrow. I treated the two burrows with tracks as occupied, which yielded a 66.7% occupancy rate. Since gopher tortoises in Florida remain either in their burrows or in the immediate vicinity during cold periods, I used this winter occupancy rate to calculate a point estimate of adult gopher tortoises in scrub habitat. Bootstrapping yielded an asymmetrical confidence interval for this small sample, which ranged from 0.381 to 0.810. When

multiplied by the upper and lower confidence intervals for the number of burrows in oak scrub, this yielded a population estimate of 682-2926, with a mean at 1731.

My simulation results (Figure 3-5) showed that if the burrow detection probability was decreased by 10% due to the obscuring effect on vision due to vegetation, our extrapolated population estimate for all 1792 hectares of oak scrub would be negatively biased by 11%. If the survey team had over-counted by 10%, the population estimate would have been artificially inflated by 9%. My simulations also showed that aggregation patterns that varied both above and below our field measurements would only have a small impact on our precision (Figure 3-6).

Discussion

Detection probability is an issue with all counting methods. The major assumption of plot-based methods is that all objects are detected. My survey team used 10 transects on 1 hectare quadrats, thus maximizing detection probability since the surveyor could observe the same semi-hidden burrow from different angles if it was located between 2 transects. With our transects spaced only 10 m apart, visibility of the burrows was excellent in the park-like oak hammock and pine habitats and was good in some early successional scrub plots. The furthest a burrow could be from each adjacent line was 5 m, and even in the denser sand pine and oak scrub plots, burrows this close could often be observed if the surveyor periodically assumed a posture close to the ground surface. In any field survey involving enumeration, complete counts are almost never made. In the study presented here, I do not claim a complete count, just a “nearly complete” count. Undercounts occur because detection probably is usually less than 100% and overcounts occur with multiple surveyors or a single fatigued surveyor; both errors introduce bias into an extrapolated population estimate. My

simulation results suggested that if these two procedural flaws had occurred simultaneously in the field (a reasonable scenario), the bias introduced by one would have partially negated bias introduced by the other. The simulations also showed that different clumping patterns which may have occurred in the field did not affect our sample precision.

There are also advantages with analysis options with this design-based approach. First, biologists and statisticians are well-familiar with the statistical literature on finite sampling. Secondly, if count data is available from other parts of the species' range, it could be used as a prior distribution, allowing a researcher to take advantage of Bayesian statistics. Since biological count data is frequently distributed as a negative binomial, the likelihood ratio testing approach illustrated here models differences in the variances reflected by the k parameter of this distribution with the intent of gleaning additional biological information (White and Bennetts 1996). The extra information gained here was that gopher tortoises dig their burrows in about the same spatial pattern in these habitats, they just dig considerably more burrows in oak scrub. Thus, an additional advantage of this method is that it provides data on dispersion as well as counts.

Almost all of the scrub patches sampled in the northern half of APR contained burrows and many of these patches were small, $< 1 \text{ km}^2$. My results confirmed the empirical finding of McCoy and Mushinsky (1995) that smaller areas of tortoise habitat tend to have higher densities of burrows than larger areas. The gopher tortoise responds not to any particular plant association, but rather the physical characteristic of the habitat (Campbell and Christman 1982), and these small patches usually possessed the 3 habitat features required by this species (well-drained loose soil in which to burrow, adequate low-growing herbs for food, and open sunlit sites for nesting; Auffenberg and Franz 1982). This data on habitat use

should be useful in conservation planning of this imperiled species, since the state of Florida is purchasing tracts of land under the Conservation and Recreational Lands (CARL) program.

Although the wide confidence interval around the point estimate of 1731 adult tortoises indicates some imprecision in my measurements, the estimate is probably unbiased, for several reasons. First, I followed the time-honored sampling principles of “stratify, randomize and replicate” (Green 1979). Randomization reduces bias, and stratification with replication increases precision. I sampled without replacement, which yields unbiased estimates, and is the preferred technique for assessment of biological populations (Thompson et al. 1998). With the randomized design approach, both point estimates and variance estimates can be assumption-free (Borchers et al. 2002); it was not necessary to assume the tortoises burrows were distributed uniformly or independently in each stratum. Since little was known *a priori* about the population of tortoises on this military installation, it was “reassuring to know that the estimation method used is unbiased no matter what the nature of the population itself” (Thompson 2002). The non-parametric bootstrap I used to calculate confidence intervals does not depend on independence of burrow locations, and since several burrows counted on a plot are often dug by the same tortoise, it is likely that burrow locations were not independent. The bias-adjusted method I used is considered more accurate with skewed data than standard bootstrap methods and should provide coverage closer to the assumed coverage over a broad range of parent distributions (Efron and Tibshirani 1993). Working with similar data (a low density possum population in New Zealand that fit a negative binomial distribution), Brown and Thomas (2000) found that the bias corrected bootstrap provided better coverage and balance than the standard bootstrap. Moreover, having an asymmetrical confidence interval is a good property with skewed data, as long as

the center of the interval is correctly located (Thompson et al. 1998). Since I used random procedures to select plots and my spatial coverage of scrub encompassed most parts of APR, the center of the interval is likely unbiased.

This study makes two contributions. First, it directly contributes to the conservation of the gopher tortoise, and the species that use its burrows. The plot-based method presented here should work better in situations where line transects would frequently intersect other vegetation types in irregular shaped patches or could inadvertently be placed on a systematic pattern of objects to be sampled. Although distance sampling could be used in small, irregularly shaped patches of vegetation, it's the *implementation* in the field where I believe my method is advantageous. Since the habitats I sampled at APR also occur throughout central Florida, the procedure outlined here should be useful for sampling other tortoise colonies where density is low. Unfortunately, such habitats with sandy soils are being dramatically reduced in Florida, and there is an urgent need to assess populations in different areas. To do this, biologists need to use a method appropriate to the local situation. In larger areas of more open terrain where the assumptions of distance sampling can be met, distance sampling should be used to sample burrows. However, this species will readily dig burrows in a systematic pattern in small, irregularly shaped strips of thick vegetation along the edges of upland terraces. I provide a statistically-based, standardized survey protocol to sample tortoise burrows, for biologists responsible for managing this species in such terrain, along with a modest simulation method to review the effects of under- and overcounts. Additionally, this is the first study that quantified the clumping of gopher tortoise burrows, showing that they follow the negative binomial distribution. Such basic ecological knowledge on spatial distribution is needed to manage any species.

Secondly, the conceptual framework outlined here could be used to analyze vertebrate animal sign such as burrows, or slow-moving or sessile invertebrates. If additional funding becomes available, the study design could be upgraded to estimate patch occupancy (MacKenzie et al. 2006), using the set of randomly chosen quadrats as the “occasion 1” set of quadrats. However, funding for repeat visits is not always possible, and the framework outlined here should be applicable when funding only allows one visit per site.

Table 3-1. Summary statistics for Gopher tortoise burrow quadrat study conducted in four upland habitats at Avon Park Air Force Range, 1997-98. Field data values listed with re-sampled values in parenthesis below. Legend: OS: oak scrub; PF: pine flatwoods; SP: sand pine; OH: oak hammock; C.I. _R : confidence interval (2.5 and 97.5 BCa percentiles) for 1000 resamples.

	OS	PF	SP	OH
Number of plots	55	53	23	17
Number of active burrows	81	24	4	8
Sample mean	1.473	0.453	0.174	0.471
C.I. _R	1.018, 2.050	0.226, 0.698	0.044, 0.348	0.588, 1.471
Total hectares habitat	1762	25275	518	879
Estimated population size in strata	1761-3588	5722-17657	23-180	0-1034
Standard deviation	2.026	0.868	0.388	1.281
Range	10	3	1	5
Proportion of plots with burrows	0.582	0.264	0.174	0.176
C.I. _R	0.418, 0.691	0.132, 0.377	0.044, 0.304	0, 0.353
Index of dispersion	2.78	1.66	0.868	3.484
Green's Index	0.0223	0.0276	-0.0455	0.3549

Table 3-2. Likelihood ratios tests comparing four negative binomial models of tortoise burrow dispersion to determine if differences exist in m , k , or both.

General Model	Reduced model	LRT	df	P
$\{k, m_v\}$	$\{k, m\}$	21.672	3	0.0001
$\{k_v, m\}$	$\{k, m\}$	8.301	3	0.0402
$\{k_v, m_v\}$	$\{k, m\}$	26.941	6	0.0001
$\{k_v, m_v\}$	$\{k, m_v\}$	5.269	3	0.1531
$\{k_v, m_v\}$	$\{k_v, m\}$	18.640	3	0.0003

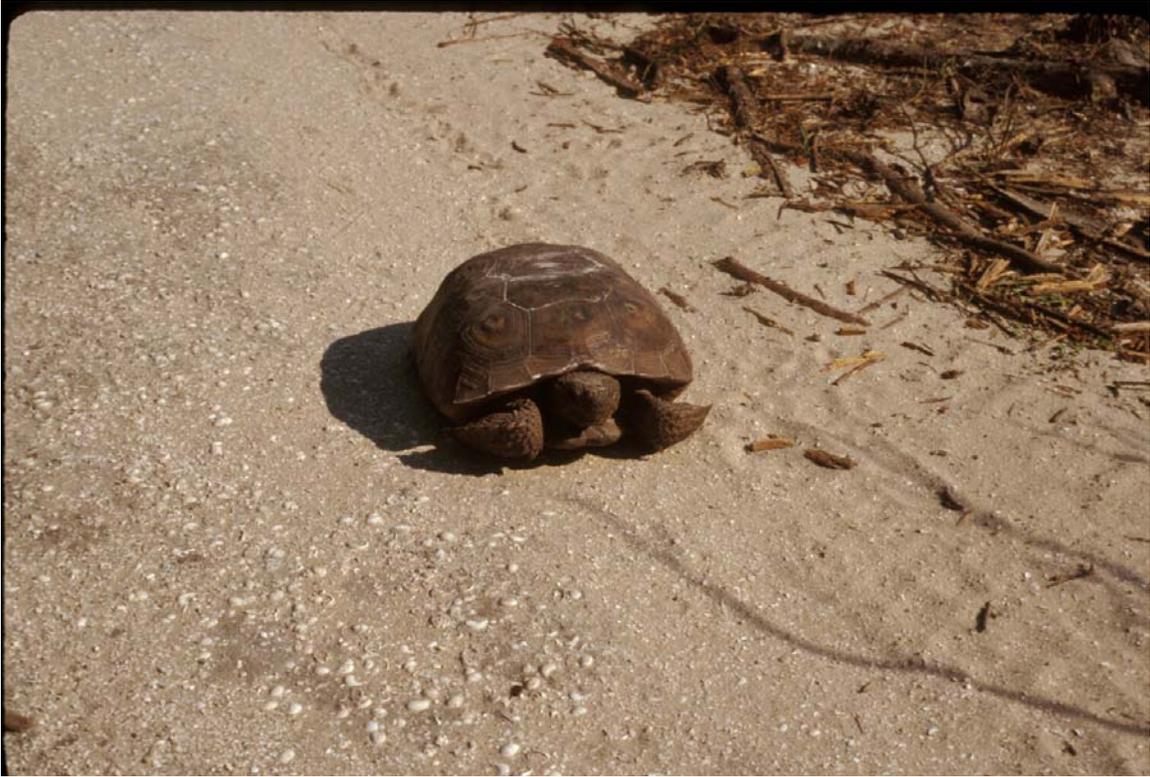


Figure 3-1. Gopher tortoise (Gopherus polyphemus) walking.

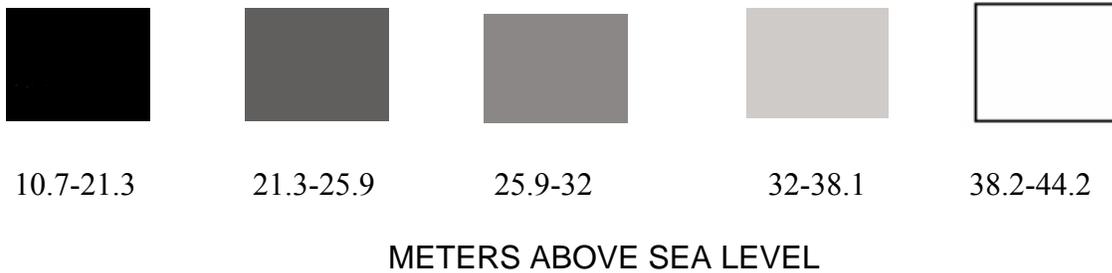
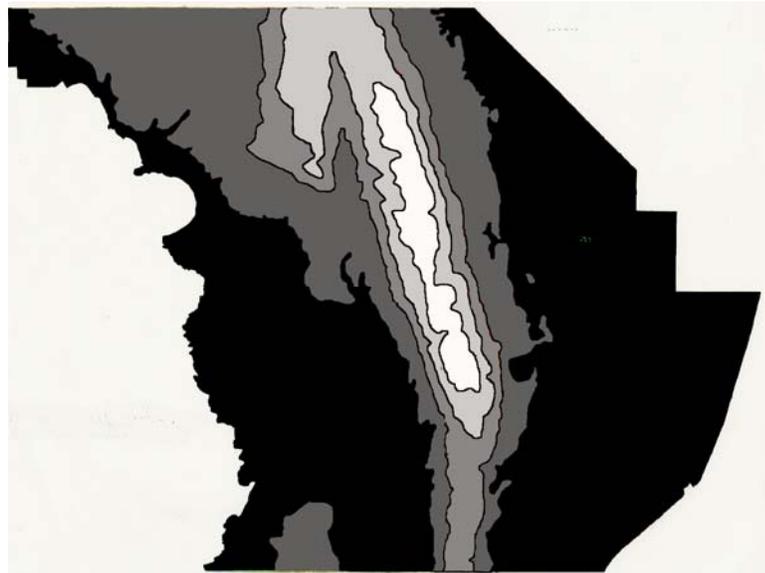


Figure 3-2. Contour map of Avon Park Air Force Bombing Range. The major topographic feature is the north to south trending, sand ridge, ranging in elevation from about 53.3 m. above sea level at the highest point, represented by the white and gray areas in the central part of the Figure, down to about 21.3 m., represented by black. Gopher tortoises occupy the upland vegetation zones that occur in the deeper sands of the ridge, but also occur in sporadic patches of deeper sand found at lower elevations, represented by black. Modified from a GIS map provided by Peg Margosian, APR.
Legend:

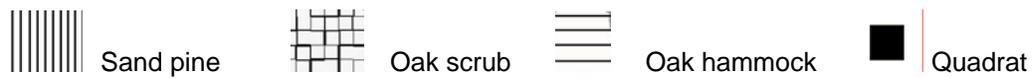


Figure 3-3. Location of random 1 hectare quadrats along the Frostproof Road area of Avon Park Air Force Range during quadrat survey, 1997-98. Open area to left is northeast section of Lake Arbuckle. In this figure, 3 plots are located in oak hammock, 3 in sand pine, and 5 in oak scrub. No pine plots are illustrated. Note grid overlay. Areas in gray are mesic habitats not sampled.
 Legend:

Observed Data vs Negative Binomial Fitted Data

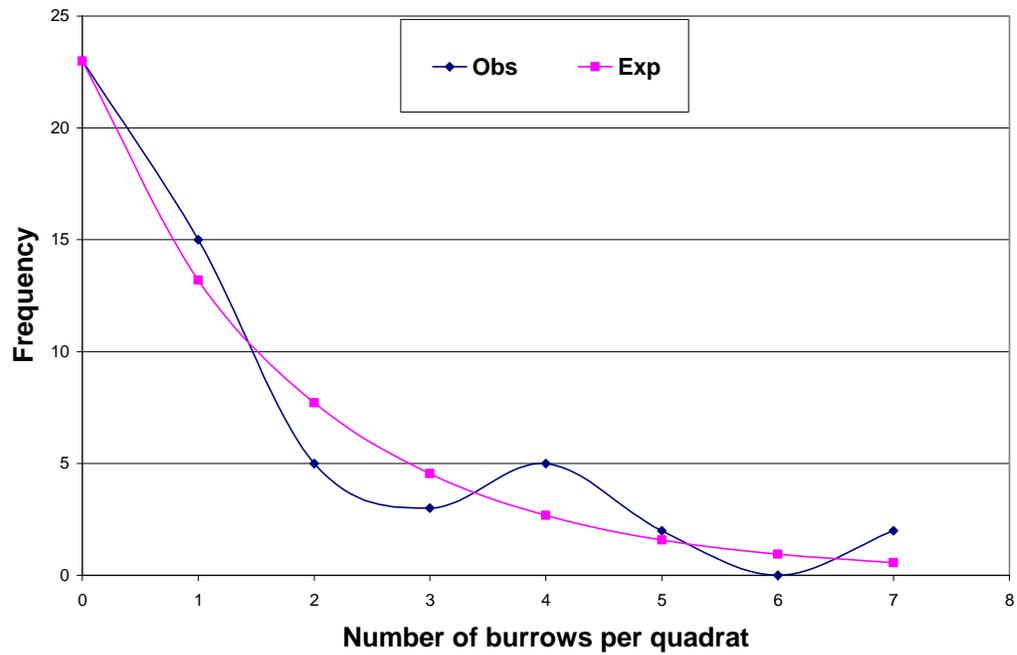


Figure 3-4. Frequency count of gopher tortoise burrows surveyed in arid oak scrub versus count expected by the negative binomial distribution. Burrows were surveyed at Avon Park Air Force Range, Florida, in 1997-98.

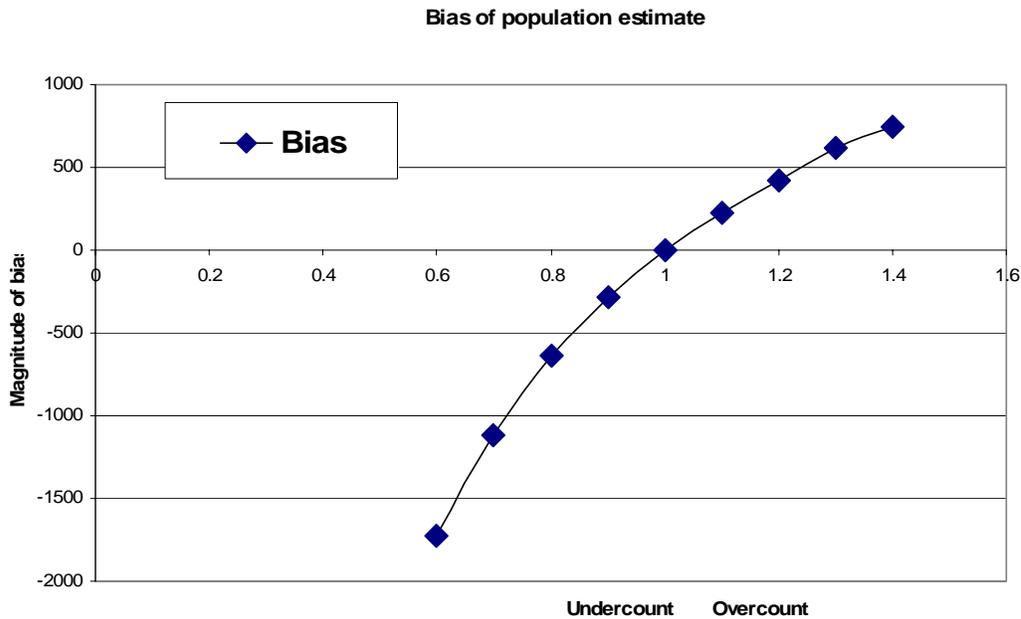


Figure 3-5. Bias of extrapolated population estimate of active tortoise burrows in 1762 hectares of oak scrub habitat. This bias would occur if surveyor undercounted (by a factor of 0.6, 0.7, 0.8, or 0.9) or over-counted (by a factor of 1.1, 1.2, 1.3, or 1.4) the “true” number of burrows, resulting in a sampled count of 81 burrows counted in the field on 55 randomly selected plots at Avon Park Air Force Range, Florida. In this simulation, the “true” extrapolated population size is 2595.

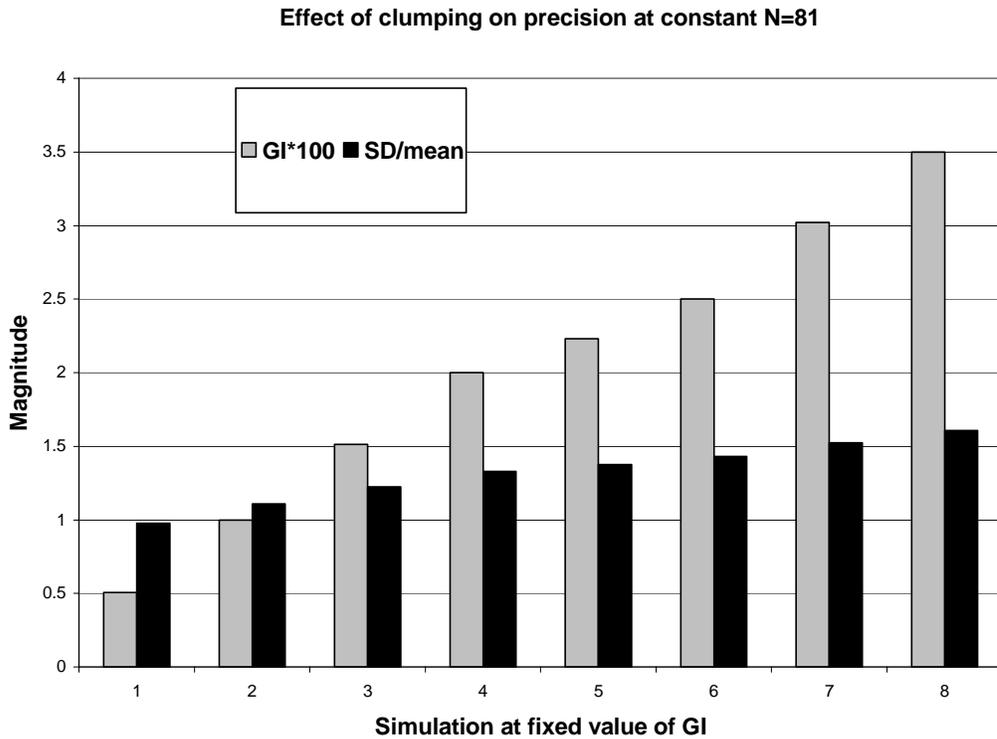


Figure 3-6. Effect of clumping of burrows on precision of sample abundance estimate in a quadrat sampling survey at Avon Park Air Force Range, Florida. Precision is measured as standard deviation divided by mean. Clumping measured as Green's Index [$(ID - 1)/n - 1$, where $ID = \text{variance}/\text{mean}$]. The index values examined are 0.005, 0.01, 0.015, 0.02, 0.022, 0.025, 0.030, and 0.035. Simulation number 5, the actual field value of 0.022, is listed for comparison. The Green's Index values were multiplied by 100 for graphing purposes; the precision (S.E./mean) of each data array is graphed beside each constrained GI value, see text for details. The graph shows that different dispersion patterns likely to be found in the field would have little effect on the precision of our sample estimates.

CHAPTER 4 BURROW DISPERSION OF ARMADILLOS IN CENTRAL FLORIDA

Introduction: Armadillo Life History

The nine-banded armadillo (*Dasyus novemcinctus*, Figure 4-1) is a very adaptable mammal (Kays and Wilson 2002) in that it occupies many habitats and is reported to be increasing its range 4-10 km/yr in the southeastern United States (Humphrey 1974). Since the 1900's they have completely invaded Texas through natural range expansion from Mexico (Davis and Schmidly 1994). Florida armadillos are derived from two sources: introductions in south Florida (Bailey 1924, Sherman 1936) and recent natural expansions into west Florida from the west. (Humphrey 1974). Presently they are well established throughout Florida with the exception of the wetter parts of the Everglades (Neill 1952, Taulman and Robbins 1996). Armadillos are commonly associated with human activity and are one of the most common road-killed mammals found along Florida's roadways (Inbar and Mayer 1999).

This recent invasion has brought armadillos into contact with gopher tortoises (*Gopherus polyphemus*), a large fossorial chelonians that digs extensive underground burrows in pyrogenic ecosystems of the southeastern United States. *G. polyphemus* is listed as a Species of Special Concern by the Florida Game and Fresh Water Fish Commission (Wood 1996) and is considered "vulnerable" to extinction by IUCN. Although there is no information on what impact armadillos have had on this tortoise, the ecology of these two species are intertwined. Guyer and Hermann (1997) speculated that the availability of gopher tortoise burrows and their subsequent use by armadillos may have played a role in local armadillo dispersal. Galbreath (1982) observed that an armadillo was aggressive to a tortoise

when the two were confined together. In view of the tortoises' decline, data on armadillo habitat use patterns is needed to understand better the interaction between the two species and formulate management plans.

Regional distribution of armadillos in Texas is related to soil texture, with sandy soil preferred (Taber 1945), and marshy areas of excess water avoided (Davis and Schmidly 1994). Local distribution of armadillos in Florida is related to the abundance of the insects they consume, which are in turn related to rainfall and season (Wirtz et al. 1985).

In this study, I used burrow counts as a metric to measure habitat occupancy. This is well justified since burrows play a major role in the functional ecology of this species (Clark 1951). Armadillos use burrows for thermoregulation (Gause 1980, McNab 1980), predator escape (Breece and Dusi 1985), and as food traps (Taber 1945). Moreover, an individual armadillo can save the energy and time required to dig its own burrow by occasionally usurping a burrow dug by another species. Since they are much more likely to dig burrows in regularly used habitats within their home range (McDonough et al. 2000), burrow counts should reflect an accurate measure of use by armadillos of preferred habitat.

Armadillo burrows are easily counted. Counts of such biological populations or objects often fit the negative binomial distribution (NBD; Bliss). Although the application of the NBD to animal populations was described over 30 years ago by Elliott (1971), it has been underused in practical conservation strategies. A characteristic of the NBD is that frequencies can decrease monotonically from a modal value of zero (Pielou 1969), which may describe burrow distribution. The NBD is described by two parameters: the arithmetic mean (m) and a dispersion parameter (k). The reciprocal of the dispersion parameter ($1/k$) is interpreted as the degree of clumping in the population (Krebs 1999).

The use of counts of animal artifacts such as tracks, pellets, nests or burrows as a crude index to population size has a long history in wildlife management (Overton 1971; Sutherland 1996). For the index to be used to estimate population size, it must be calibrated by determining the relationship of the true population density with the density of the artifact (Caughley 1977). At the end of the paper, I discuss the issues involved in using burrow counts as a population index with *D. novemcinctus*.

Study Area

The Avon Park Air Force Range (APR) is a 106,074-acre military reservation located in Polk and Highlands counties, Florida and is used as an active bombing range. APR consists of a mosaic of upland and wetland communities, but the major topographic feature is a sand ridge, oriented north to south, 175 feet above sea level at the highest point, grading down on the east and west sides to about 70 feet above sea level. The ridge is referred to as the “Bombing Range Ridge”, a classic “drum-stick” barrier island, thought to have developed during an early Pleistocene marine regression (White 1970).

Methods

This 1997-1998 survey had a stratified random design (Cochran 1963). A transparent overlay with a grid of numbered squares was applied to a GIS map of the plant communities of Avon Park, with the scale set so that each square drawn on the map represented a 1 hectare plot in the field. Using a random numbers table (Steel and Torie 1980), 55 plots in oak scrub, 53 in pine flatwoods, 23 in sand pine scrub, and 17 in oak hammock were randomly selected. No effort was made to detail the activity status (currently used versus not currently used) of the burrows. The survey did not include a few habitats that might be used by *Dasyus*, including managed pine plantations, cypress, marsh-wet prairie-lake edge, pastures,

hardwood swamp forest, or ruderal sites. The pine flatwoods category combined mesic and scrubby flatwoods. Each plot was then located in the field and thoroughly searched for both gopher tortoise and armadillo burrows by one, two, or occasionally three surveyors. Three criteria were used to distinguish burrows of the armadillo from those of the gopher tortoise. The first criterion was the difference in shape of the opening: active Dasypus burrows have a vertically ovoid shape, whereas active Gopherus burrows have a horizontally elliptical (“half-moon”) appearance, reflecting the body shape of each excavator. Secondly, tortoise burrows had a considerable “apron” or mound of freshly excavated sand opposite the entrance; the soil excavated by armadillos was not nearly as extensive, as they do not usually excavate as much soil, resulting in shallower burrows. Thirdly, tracks of each species were often found at the burrows and have fundamentally different shapes. The rounded tortoise tracks are usually abundant inside the burrow tunnel and at the opening of an active tortoise burrow, as well as on or around the apron. The “hoof-like” armadillo tracks are distinctive when seen in soft sand at the opening. Although armadillos will construct above ground nests (Layne and Waggener 1984), these were not sampled in this study.

In analyzing the data, summary statistics included point estimates and 95% confidence intervals for the mean burrow count per quadrat and the sample proportion of burrows in each habitat. Confidence intervals for means were obtained by bootstrapping (Efron and Tibshirani 1986) the data, rather than using transformations, because the normality assumption did not hold for these skewed data and because of small sample sizes for two of the habitats.

Habitat and burrow counts were tested to see if there was an association between the two, using Pearson’s chi-square statistic. The odd’s ratio (probability of success divided by

the probability of failure, for one habitat compared to another habitat) was calculated because it is a useful statistic investigators could use to compare their chance of success in similar surveys.

Because no previous field studies had investigated the burrow dispersion of Dasypus novemcinctus, burrow distribution was plotted to determine whether or not the burrows were clumped. Since sample size was different for each of the 4 habitats, I calculated the standardized Morisita index of dispersion (Smith-Gill 1975), which is independent of density and sample size (Malhado and Petreire 2004).

Because the graph of the burrow counts (Figure 4-2) resembled a negative binomial, I tested to see if the burrows in each habitat were randomly arranged (Poisson distribution), or if they had a clumped pattern (such as the negative binomial distribution). Because the sample sizes for oak scrub, sand pine, and oak hammock datasets were too small for a chi-squared test for goodness of fit to show a negative binomial, I used a variance-mean ratio test for clumped distribution, and either a U or T statistic to test for GOF. These latter two statistics are more precise than the chi-squared test in detecting departures from the theoretical negative binomial distribution with sample sizes less than 50 (Krebs 1999). The sample size for pine was large enough to use a chi-squared test to see if the data fit the negative binomial.

I tested for equality among these different negative binomially distributed datasets, following the procedure first described by White and Eberhardt (1980). I began the analysis by testing goodness of fit to an unconstrained general model (i.e. both m and k allowed to vary, model $\{k_v, m_v\}$) of the negative binomial distribution. This provided a test of whether

the data fit the NBD without the additional constraints introduced by reducing the number of parameters.

I then used a likelihood ratio procedure to determine if there were differences in m , k , or both, using $\alpha = 0.05$, for populations of the burrows in each habitat, in the context of the NBD. Since the negative binomial can have different means (m) or different exponents (k), there were four possible outcomes (White and Eberhardt 1980):

1. each habitat differs in mean and k (model $\{k_v, m_v\}$);
2. habitats have common k but different means (model $\{k, m_v\}$);
3. habitats have common mean but different k (model $\{k_v, m\}$); and
4. all habitats have the same mean and k (model $\{k, m\}$).

Likelihood ratio tests were used to discriminate between these models. Goodness of fit between the observed data and the values expected from a NBD for each of the four models was measured using the log-likelihood G statistic (Sokal and Rohlf 1981). Since the Akaike Information Criteria (AIC) has received wide use in model selection and performed effectively (Anderson et al. 1994), I used it as an additional tool to distinguish between models. The philosophy behind this approach, as opposed to using an ANOVA or Kruskal-Wallis to test for differences, is discussed in White and Bennetts (1996) and my methodology for model comparison is a straight-forward application of their approach. Software used for data analysis include Resampling Stats (Arlington, Virginia), StatXact 3 (version 3.02), and the Quadrat Sampling program, developed by Krebs (1999, Exeter Software, Setauket, New York). For the log likelihood tests that follow White and Bennett (1996), Krebs (1999) modified the PALANL Fortran program originally written by Gary White, Colorado State University.

Results

Burrow counts showed that all four habitats were utilized by armadillos. A habitat effect on burrow counts was found (Pearson's chi square statistic 16.06, exact p-value 0.0009, StatXact 3.02). The mean number of burrows/quadrat in pine flatwoods was more than twice the density of the other habitats; however, the lower 95% (resampled) confidence interval for pine overlapped the upper 95% confidence interval for oak hammock (Table 4-1). Confidence intervals for oak scrub, sand pine scrub and oak hammock overlapped considerably. Pine flatwoods also had the highest proportion of plots with burrows. The odds of finding armadillo burrows on random quadrats in pine was 4.64, 2.95, and 4.19 that of finding burrows in oak scrub, sand pine, or oak hammock, respectively. The stratified random sample estimate of burrows in the largest habitat (pine) ranged from 31,467 to 63,920 burrows.

The variance/mean ratio was much greater than unity for all habitats, indicating a clumped distribution. The standardized Morisita Index (Smith-Gill 1975) values for oak scrub, pine, and sand pine were all around 0.5, indicating the armadillo burrows were clumped. Clumping in oak hammock was somewhat greater, with a Morisita Index value of 0.8125. A random spatial distribution was rejected for oak scrub, sand pine, and the oak hammock (p-value < 0.01 in all 3 cases). The U statistic for the oak scrub and sand pine data were each less than 2 respective standard errors, as was the T statistic for the oak hammock dataset, indicating that the negative binomial was a plausible model. However, for small datasets, the T and U statistic are approximate tests only (Krebs 1999). The chi-squared test on the larger pine dataset did not reject the null hypothesis that the NBD fit the data (chi-squared statistic 1.773, 5 d.f., p-value = 0.91).

The frequency count data for the model comparison tests are illustrated in Figure 4-2. The results of the LRT's tests suggest that the general model $\{k, m_v\}$ (i.e., k is constant but m differs) is better suited than the other reduced models (Table 4-2). Although model $\{k_v, m\}$ was marginally rejected over $\{k, m\}$, indicating some effect from k , model $\{k, m_v\}$ was not rejected over the full model ($\{k_v, m_v\}$) suggesting little effect from k . More importantly, the rejection of reduced model $\{k, m\}$ over $\{k, m_v\}$ was highly significant ($p= 0.002$), indicating that m differs (Table 4-2). My selection of model $\{k, m_v\}$ as the correct model is supported by both the GOF tests and the fact that this model had the lowest AIC scores (Table 4-3).

Discussion

The chi-squared test showed a strong association between habitat and the frequency of armadillo burrows at Avon Park, indicating that armadillos do have habitat preferences for burrow digging. The mean number of burrows/quadrat and the proportion of quadrats with burrows both indicated that pine was the preferred habitat for digging burrows in this study. The odds of locating burrows in pine were higher than the other upland habitats listed. The wide overlap in confidence intervals between oak scrub, sand pine, and oak hammock indicates that these habitats may not vary in the numbers of burrows dug.

Taber (1945) claimed that forested habitats such as pine may be preferred by armadillos because they probe for food more frequently around decaying logs prevalent in these habitats. This may not hold true for central Florida (J. Layne, pers. comm.). Unfortunately we could not evaluate this because our survey did not include detailed examinations of armadillo probings in the field.

The density of 1.7 burrows/hectare reported here is considerably less than the 42.5 reported for upland pine in northern Florida by McDonough et al. (2000). There are

probably several reasons for this disparity. A likely contributing factor is the very wet conditions that occurred during our survey. The lower Kissimmee River area (along the eastern boundary of APR) had mean rainfall of 140 cm., about 13 cm. higher than the mean (Geoff Shaughnessy, South Florida Water Management District, pers. comm.) during much of our survey period. In Florida, armadillos will shift to higher and drier terrain during periods of excess rainfall (Gause 1980); the wet conditions may have simply driven many armadillos to leave the area, resulting in a lower density on most plots and thus fewer burrows dug. An additional contributing factor may have been a decreased detection probability. Many of the pine plots occurred at lower elevations where water would often stand after heavy rains. It is very possible that many of the armadillo burrow openings may have been rapidly filled in with debris or sand carried in by the water, hampering our visibility. The resource base may have been adversely affected: flooding on some plots could have decreased the insect prey base, especially larvae stages, causing armadillos to move elsewhere in search of food. In the north Florida study, burrows were sampled during the hot summer months, when armadillos were more active and probably dug more burrows; many of our pine plots were sampled in the winter. Finally, we did not attempt to count juvenile burrows, whereas McDonough et al. (2000) did.

It was not surprisingly that my graphs closely approximated a negative binomial model. Although the standardized Morisita index showed that burrow dispersion was not random, but clumped, the LRT tests showed that this clumping did not differ between habitats. Thus, armadillos dig their burrows in about the same pattern in these habitats, they just dig considerably more burrows in pine flatwoods, a conclusion that agrees with earlier studies (Clark, 1951; Fitch et al. 1952) demonstrating a preference for mesic habitats.

Because armadillos dig multiple burrows within their home range, the method of using burrow counts as a population index is problematic (McDonough and Loughry 2001) for several reasons. Armadillos have been reported to dig different numbers of burrows in different types of soil conditions (Taber 1945). The home range of males overlaps that of females (Layne and Glover 1977, Zimmerman 1982), thus in some parts of the home range the burrow density may reflect more than one individual. Armadillos apparently dig different types of burrows, including shorter burrows used as a food probes or food traps (Taber 1945), escape burrows (Breece and Dusi 1985, Galbreath 1980), as well as typical nesting burrows (Clark 1951). The existence of these auxiliary burrows might confound any relationship between nesting burrow count and population density. Armadillos will construct above ground nests in both the Northern (Layne and Waggener 1984) and Southern (Platt et al. 2004) Hemispheres, so a count of ground burrows could not be relied on to provide an accurate index. Finally, armadillos transport grass, leaves and twigs into burrows that are to be used for nesting purposes, an activity that precludes the use of video probes for identifying active (e.g., occupied) burrows. Thus, the development and calibration of a “burrows-to-individual correction factor” for this mammal is not feasible at this time.

Although biological mechanisms cannot be inferred by fitting statistical distributions to quadrat counts, patterns seen in the data can be described (Krebs 1999). Because the relationship between burrows to individuals is not known, I cannot make any inferences about the population size of armadillos at APR. However, the data on burrow counts in the four habitats were unbiased and provide a reliable evidence for dispersion to be the same while mean values vary between the habitats (model $\{k, m_v\}$

Table 4-1. Summary statistics for armadillo burrow quadrat study in four upland habitats at Avon Park Air Force Range, 1997-98. All values listed are actual field data except confidence intervals (C.I. _R) which represent the 0.025 and 0.975 percentiles of 1000 bootstrapped samples of the dataset. Legend: Ha habitat: number of hectares of listed habitat type; Est. No. burrows: estimate of number of burrows in listed habitat; Prop. with burrows: proportion of burrows in listed habitat; SMI: standardized Morisita Index

	Oak Scrub	Pine	Sand Pine	Oak Hammock
Number of plots	55	53	23	17
Number of burrows	25	98	15	12
Mean burrows/quadrat	0.45	1.85	0.65	0.71
Variance	1.10	6.05	1.60	2.60
C.I. _R (Burrows/quadrat)	0.218, 0.749	1.245, 2.529	0.2174, 1.175	0.176, 1.588
Hectares of habitat	1762	25275	518	879
Estimated No. burrows	384-1319	31467-63920	113-609	155-1396
Proportion with burrows	0.218	0.566	0.304	0.255
C.I. _R (proportion)	0.109, 0.327	0.434, 0.698	0.130, 0.478	0.059, 0.471
SMI	0.5216	0.5072	0.5294	0.8125

Table 4-2. Likelihood ratios tests (LRTs) comparing the initial four models of armadillo burrow dispersion to determine if differences exist in m (mean), k (clumping parameter), or both.

General model	Reduced model	LRT	df	P
$\{k, m_v\}$	$\{k, m\}$	15.034	3	0.002
$\{k_v, m\}$	$\{k, m\}$	7.508	3	0.057
$\{k_v, m_v\}$	$\{k, m_v\}$	19.504	6	0.003
$\{k_v, m_v\}$	$\{k, m_v\}$	4.470	3	0.215
$\{k_v, m_v\}$	$\{k_v, m\}$	11.996	3	0.007

Table 4-3. Log-likelihood, G statistic for goodness of fit, degrees of freedom of G (probability $> G$ is denoted by P), and Akaike Information Criteria (AIC) scores for each of the four initial models used in armadillo burrow study.

Model	Log likelihood	G	Degrees of freedom	P	AIC
$\{k, m\}$	-191.415	43.55	21	0.003	388.830
$\{k, m_v\}$	-184.898	28.51	18	0.075	379.796
$\{k_v, m\}$	-188.661	36.04	18	0.009	387.323
$\{k_v, m_v\}$	-182.663	24.04	15	0.086	381.328



Figure 4-1. Nine-banded armadillo foraging.

Quadrats Counted with 0-4 Burrows/quadrat

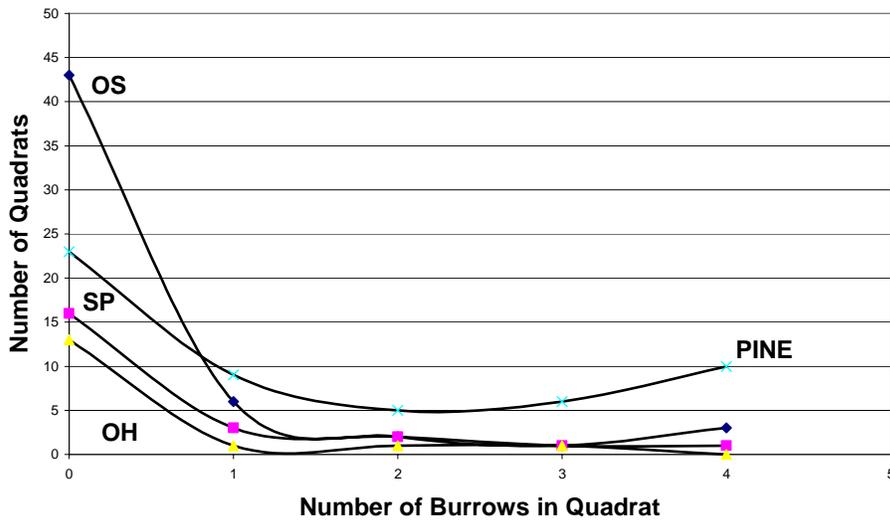


Figure 4-2. Graph of frequency count of armadillo burrows at Avon Park Air Force Bombing Range, FL, in 1997-98 in four upland habitats. Legend: OS: oak scrub; SP: Sand pine; OH: oak hammock; PINE: pine. Pine data truncated above 4 burrows/quadrat.

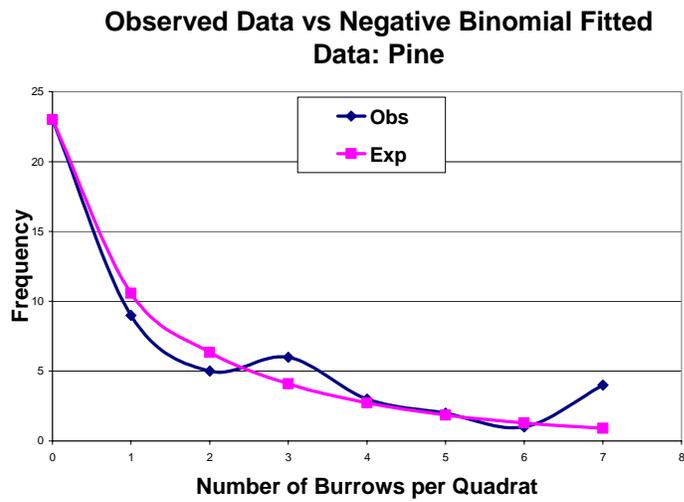


Figure 4-3. Graph of the actual pine data to that expected by the negative binomial distribution.

CHAPTER 5
ARCHITECTURE OF GOPHER TORTOISE BURROWS
DETERMINED BY 2D GROUND PENETRATING RADAR

Introduction: Gopher Tortoise Burrows

The gopher tortoise (Gopherus polyphemus) is a large fossorial chelonian, averaging 23-28 cm in carapace length. These tortoises constructs extensive underground burrows in pyrogenic ecosystems of the southeastern United States, especially favoring the sandhill and scrub vegetative communities (Auffenberg and Franz 1982; Diemer 1992). Because at least 362 species of vertebrates and invertebrates have been reported to use these burrows at some stage in their life or seasonal cycle (Jackson and Milstrey 1989), the gopher tortoise has been referred to as a keystone species (Eisenberg 1983). Gopher tortoise burrows vary in diameter, depth, and complexity and play a critical role in the ecological processes of sandhill and scrub communities of Florida. They impact geomorphology (Butler 1995), soil dynamics (Gardner and Landers 1981), vegetation patterns (Kaczor and Hartnett 1990; Tuberville, 1998), animal community diversity (Milstrey 1987 for invertebrates, Franz 1986 for vertebrates), and possibly hydrology, at scales ranging from microsites to landscapes. Some species, such as Florida mice (Podomys floridanus; Jones and Franz 1990), eastern cottontail rabbits (Sylvilagus floridanus; Kinlaw 1999) and armadillo (Dasyopus novemcinctus; Guyer and Hermann 1997) will modify tortoise burrows for their own needs, adding complexity over time. Recognizing that Gopher tortoise populations are in a decline throughout the species' range, the Florida Fish and Wildlife Commission (FWC) is currently reclassifying the tortoise from it's present status as a Species of Special Concern (FWC 2004) to a Threatened status (FWC 2006a), along with strengthening protection of it's burrows (FWC 2006b).

Data on the internal geometry of a burrow can be obtained using simple measurement tools such as calipers, calibrated flexible rods, or by measuring dimensions of casts of burrows made from hardening agents. On sites slated for development, Gopher tortoises are collected by excavating their burrows using heavy equipment (Blankenship and Thomas 2005). Although general information about the depth and extent of burrows can be learned by this method, it destroys burrows, along with any opportunity for repeat measurements of burrow geometry. With excavation, any beneficial ecological effects of the destroyed burrow are lost. Invasive probing methods can cause burrow abandonment or behavioral disruption of the burrow inhabitants (pers. obs., A. Kinlaw). Some success in understanding underground burrow structure for other animals has been achieved in the United Kingdom using geophysical methods. Butler et al. (1994) were successful in determining size for six badger (Meles meles) setts using soil resistivity but were unsuccessful using magnetometry. Any approach to modeling changes of burrow structure over time, such as Meadow's (1991) model, which is based on tortuosity and complexity, requires a method to image burrows that is non-invasive, repeatable, and relatively quick. One such approach is ground penetrating radar.

Ground Penetrating Radar Methodology

Ground penetrating radar (GPR) is a non-invasive subsurface imaging technology which uses a surface antenna to transmit electromagnetic energy pulses in the form of radar waves, downward into the ground (Conyers 2004). Waves of varying amplitudes are then reflected back from buried interfaces to a receiving antenna, which is assembled together with the transmitting antennae on a movable sled or cart. The time elapsed between transmission and reception, the amplitude and phase of the received waves, and the frequency of those

waves are recorded on the hard drive of a computer which interfaces with the antennas. Of the waves reflected back from buried interfaces, the largest amounts of energy are reflected back from highly contrasting media. In the case of air-filled burrows, a good deal of radar energy is reflected from the interface between the sandy sediment and the void of the burrow itself; other reflections can occur from tree roots, shallower burrows of other animals and sedimentary or soil beds. As the sled is slowly moved along pre-determined surface transects, a series of reflections can be collected at a programmed distance, determined by the revolutions of a survey wheel attached to the sled (Fig. 5-1). All reflections are collected in radar travel times measured as two way-travel time in units of nanoseconds. These times can be converted to approximate depth in the ground when the velocity of the radar energy travel is calculated. When many hundreds of these reflections from varying depths are stacked and viewed in a two-dimensional vertical profile, a “cross-section” of the ground is produced.

Radar energy propagation occurs best in dry sandy soils, however good penetration also can occur in a number of other ground conditions (Conyers 2004). The applicability of GPR to locate cavities such as pipes or tunnels was recognized in the 1970’s (Fullagar and Livleybrooks 1994). Since air-filled voids provide an excellent dielectric constant contrast (Daniels et al. 1992), GPR is recommended by the Association of State Dam Safety Officials (ASDSO 1999) to identify animal burrows in earthen dams in the United States which might cause collapse of the dams.

Field Site Description and Burrow Selection

Three study sites were located in the Ocala National Forest, Marion County, Florida. The sandhill site (Kerr) is located along the north shore of Lake Kerr, in the Lake George

District of the Forest. The two oak scrub sites were located adjacent to the US Naval Reservation in the Seminole District of the Forest.

In Florida, sandhill vegetative communities are rolling park-like woodlands of longleaf pines (*Pinus palustris*) rising above a continuous cover of wiregrass (*Aristida stricta*) with other grasses and forbs, and occasional clumps of deciduous oaks, mostly turkey oak (*Quercus laevis*; Myers 1990). Visually, sandhills are open and one can often see for a hundred meters or so. The soil type at the Kerr site is Astatula sand (AtB). This is an excessively drained soil with a dark-gray or grayish-brown sandy surface layer above yellowish, sandy layers that extend to a depth of 80 inches or more, with a water depth of 60 inches or more. Uncut sand pine scrub is a vegetative community of tall, twisted, leaning sand pine (*Pinus clausa*) rising above a thick understory of evergreen scrub oaks (*Q. geminata*, *Q. myrtifolia*, *Q. inopina*, *Q. chapmanii*), Florida rosemary (*Ceratiola ericoides*), interspersed with rusty lyonia (*Lyonia ferruginea*), scrub holly (*Ilex opaca* var. *arenicola*), silk bay (*Persea humilis*), and scrub hickory (*Carya floridana*; Myers 1990). However, scrub vegetation often has open areas. The soil type was Astatula sand (AsB), an excessively drained, sandy soil occurring on broad, undulating ridges, with a water table always below a depth of 60 inches (Aydelott et al. 1968). The GPR scrub sites had been logged within 10 years previous to this study, thus the sand pine trees were between one and five meters high. The soil order in both sandhill and sand pine scrub vegetation is classified as entisols, dominated by gently sloping, well-drained thick sands (Brown et al. 1990). These excessively drained soils are derived from quartz sand (Brown, et al. 1990) and are mostly devoid of silt and clay.

These plots and burrows were chosen as part of another of my research projects. Many sandhill plots were available, thus a map of this vegetative community was gridded into one hectare squares and each square assigned a number. The plots were then selected using a random numbers table (Steele and Torie 1980). Gopher tortoises seem to prefer sand pine scrub areas that have undergone succession three to five years after a clear-cut, so the scrub plots were chosen from the few appropriately aged plots available. I tried to select only burrows that appeared to have been recently dug or were actively being used by the tortoises, since the literature indicated that these provided the most biological insight.

Prior to testing with GPR all burrows were examined with an infrared video probe camera attached to a 7.7 m section of polybutylene tubing (assembled by Edward E. Wester, Southern Ecosystems Research, 6485 Lee Road 54 Auburn, AL 36830). This examination found that six of the burrows each contained a tortoise. The length of four others exceeded the length of the camera tether and occupancy could not be confirmed, but recent tracks, skid marks, and other surface signs indicated obvious use within a day or two prior to this testing. Finally, four burrows had sign that was somewhat deteriorated and did not have a resident tortoise (Table 5-1). Under the current scheme in use in the southeast to classify the status of gopher tortoise burrows (Auffenburg and Franz 1982), ten would be classified as “active” and four as “inactive”.

GPR Collection Procedure

The GPR antennae at the test sites were first calibrated for ground conditions that were often unique to each area. This included setting automatic range gain settings to enhance the reflection amplitudes with depth due to normal energy attenuation in the ground (Conyers 2004). A time window was selected, measured in nanoseconds, which preliminary

velocity tests showed to be consistent with the maximum depth of the burrows. This time window varied between 50 to 70 nanoseconds, which corresponded to a maximum energy penetration depth of about 4 to 5 meters. Optimal energy penetration occurs when the antennae are in direct contact with the ground surface at all times (Conyers 2004). To facilitate this, approximately 20-80 m² of vegetation immediately above each burrow was mowed. I then followed a two step procedure to map the burrows in the field. First, each burrow was probed with a piece of flexible electrical conduit to determine its beginning direction and maximum extent. Then, using a 900 MHz frequency antenna (Geophysical Survey Systems, Inc, 13 Klein Drive, PO Box 97, North Salem, NH 03073-0097 USA), I collected a series of “trial and error” transects at orientations estimated (from the initial probings) to be perpendicular to the burrow. In this way radar reflections when viewed in profile would produce a hyperbolic shaped reflection, with the apex of each hyperbola denoting the top of the burrow tunnel. The location of each hyperbola apex was marked with a pin flag at the ground surface immediately over the section of tunnel that had just been crossed by the GPR antenna. This preliminary process of profile collection and immediate interpretation was continued until an approximate burrow path was delineated by flags, and then its total extent was marked with spray paint. During this preliminary step it was quickly determined that most burrows were not straight, but angled quickly from the surface as they continued down to greater depths. When many reflection profiles were collected in this way and viewed on the computer screen in “real time”, the depth and orientation of the burrow void spaces could be determined. Often this process was confusing, as shallower burrow reflections, tree roots and the complex nature of reflections from curving tortoise burrows that

often reached three and a half meters in depth produced an array of reflections with many different orientations.

Following Stott (1996), I wanted to verify that the hyperbole reflected by the GPR antenna was in fact the subsurface tortoise burrow I believed I was imaging, not a different burrow, unknown air void, or a sampling artifact. During this pilot step, I confirmed that the GPR antenna was actually imaging the burrow path by examining the section of tunnel directly underneath with the video probe camera slid down the tunnel. By treating the vertical distance between the antenna and the burrow immediately below the antenna as side A of a right triangle, and the horizontal distance between the antenna and the burrow entrance on the ground surface as side B of the triangle, I used the Pythagorean Theorem to calculate the correct distance (hypotenuse) to slide the camera down the burrow to be immediately underneath the antenna. This confirmation step was only conducted near the entrance of the first few burrows I imaged before the burrow curved.

To accurately map the depth of the burrows, I conducted a velocity analysis to calibrate the relationship between radar travel time and depth. At several locations along the first three burrows I processed, a calibrated steel rod was inserted from the ground surface to the top of the burrow; the point of insertion into the burrow could be determined by a relaxation of insertion pressure as it entered the void space. Correct placement of the rod in the burrow chamber was confirmed by observation with the video-probe camera. These depths were then measured and the elapsed radar time measured in the GPR reflection profile at that location was then obtained. In these tests an average radar travel velocity was calculated to be 8 centimeters per nanosecond. Using this average velocity a two-way radar travel time of 45 nanoseconds was equivalent to approximately 3.6 meters in the ground.

This velocity was used to convert all measured times of burrow reflections to depth at all test sites. For all the sites tested this average velocity appeared to be consistent, which is understandable as all the burrows tested were found in the same type of dry aeolian sand. Ground moisture conditions, which can sometimes dramatically change radar velocities, were similar during GPR data acquisition. By following this process, an accurate depth profile of each burrow was made.

In the second step, a rectangular grid was then arranged over the total extent of each burrow with tape measures and their surface extent was mapped as x and y coordinates, measured from the southwest datum of each grid. The GPR antennae were moved in four meter transects perpendicularly across the burrow to collect reflection profiles normal to the orientation of the burrow (Fig. 5-1). The middle of the profile (at about two meters) therefore denoted the approximate center of each burrow, no matter what its depth. Reflection transects were placed every 50 centimeters along each surface-outlined burrow in this second step, which was a more formal process than the preliminary trial and error step. Paint and surveyor flags were used to mark the orientation and extent of each burrow (Fig. 5-2), and photographs were taken. In this fashion the x and y coordinates of the burrow were determined from the surface measurements with z values (depth) obtained for each profile by measuring from the surface down to the apex of each reflection hyperbola (Fig. 5-3). On each burrow, I made a final longitudinal transect along the ground surface that followed the path of the burrow; the resulting profile illustrated the gradual vertical drop of the burrow as the antenna moved (Fig. 5-4).

Image Analysis

Data points were transferred to two programs which translate three-dimensional spatial data into visual displays. Slicer-Dicer (Pixotec, LLC, 15917 S.E. Fairwood Blvd, Renton Washington 98058, USA) is a program that allows the user to visualize three-dimensional data as a projected volume. This program creates isosurfaces from the data, meaning that the interfaces producing the GPR reflections are placed in three dimensions, and a pattern or color is assigned to specific amplitudes in order for them to be visible (Heinz and Aigner 2003). The second program, FormZ (Auto·des·sys, Inc. 2011 Riverside Drive, Columbus, OH 43221), is a general-purpose solid and surface modeler with which the user can generate highly articulated renderings of most three-dimensional forms from x, y, and z data. To determine how accurately these renderings describe real burrow geometry, I compared them with physical casts of burrows prepared at a Clermont, FL site where the burrows were being excavated for relocation purposes, with photos taken during these burrow excavations, and with one literature account.

Results

The two dimensional outlines on the ground surface showed that nine burrows turned to the left within two to three meters of their opening, three turned right, and one was fairly straight (Table 5-1). Data were incomplete for one burrow which had collapsed about three m from the entrance. A 3-dimensional profile was developed for one burrow using the Slicer-Dicer visualization program, showing a downward corkscrew turn to the left (Fig. 5-5). Three-dimensional profiles were developed for four burrows using the FormZ modeling program, which showed the burrow tunnels had smooth sides, some up and down loops or twists, and an overall “jagged” corkscrew shape (Fig. 5-6). Examinations of hardened foam

burrow casts and photos from the Clermont relocation site confirmed that those burrows had the same properties.

Discussion: Advantages and Limitations of GPR

This research provided the first intact visual views of gopher tortoise burrows. The 2-dimensional outlines on the ground surface show that most burrows investigated in this study turn in some fashion. The 3-dimensional profile showing a corkscrew shape coincides with observations by Smith et al. (2005) for burrows that were excavated during a drought in east-central Florida. They reported burrows which angled down in a corkscrew fashion and attributed this to tortoises digging until they reached a cool hardpan layer under sand during the drought. Moreover, I compared the appearance and orientation of the FormZ three-dimensional renderings with actual hardened foam casts of burrows indicates that the models developed with this program accurately compares with the orientation and shape, including turns, of real burrows. Since the resolution of the GPR system I used was not detailed enough to image smaller side tunnels or rough surfaces along the side of the main tunnel, these features would not be represented in the visualization programs. Although the FormZ program smoothes the surface of a tunnel, this did not affect my results, as my burrow casts show fairly smooth surface features. These foam casts were taken in an area without shrubs or trees; I caution that the sides of burrows occurring in areas with more roots may not be as smooth. The longitudinal GPR profiles produced at each site clearly show burrows descending into the ground, sometimes leveling out, and again descending to their end. The FormZ models illustrate well both the up and down undulations of the burrows, as well as the turns, and the foam casts confirmed that these features occur in real burrows. All bio-mathematical models are approximations, and there is no reason why my three-dimensional

renderings of burrows should be different. Thus, comparisons with features of real burrows show that these visualization programs using GPR data do provide reasonable models of burrows.

Ground penetrating radar can assist with practical conservation efforts of the gopher tortoise. Gopher tortoises occur in a number of national forests and military reservations throughout the southeast. GPR could be used to assess or estimate the damage caused by heavy equipment, such as forestry skidders or military tanks, which can cause the collapse of burrow entrances. Gopher tortoises will also dig burrows in suitable soil occurring on cattle ranches. Trampling by cattle can collapse the opening or shallower sections of burrows, especially in overgrazed areas (pers. obs., A. Kinlaw). The single collapsed burrow found in this study was encountered very early in this study and I did not attempt to thoroughly map it. However, subsequent mappings demonstrated that intact tortoise burrows could be imaged even if the entrance was completely sealed, because the GPR ground profiles showed other burrows underground (near the imaged burrows) that could be traced to old soil mounds.

By imaging the internal architecture of burrows, GPR technology could clarify issues relating to energy expenditure in building the burrows, flooding of burrows, respiratory environment, and amount of living space for invertebrates and commensal vertebrates. By collecting a time series of profiles at the same burrow, changes in the architecture of a burrow can be better understood, as well as changes in architecture brought about by other animals that modify a burrow.

There are many advantages of using GPR for mapping and visualization of burrows. Like any good scientific method, GPR mapping is repeatable. A major advantage is its non-destructive abilities. Although the environmental impact of mowing a small amount of

vegetation at the surface immediately above a burrow is not known, none of the burrows or entrances was physically impacted in any way using this technique. The method is non-invasive to the interior of the burrow; all the work is done at the surface. Finally, the digital format allows the data to be analyzed using a variety of approaches.

Presently the only other method available to obtain an image of a burrow is to fill a burrow with some type of material that hardens into a 3-dimensional mold of the burrow shape, then excavate the mold. Although excavations are normally conducted to relocate gopher tortoises, it can be part of a process to map burrows, as in my Clermont foam study mentioned above. Although the time spent in the field with each activity was roughly comparable, mapping by excavation is an inefficient and crude technique compared to GPR. With GPR, I tested 14 sites in 8 field days, spending three to four hours at each site, including set-up time. Practically any burrow could be selected; with the excavation method only burrows listed on a State-issued permit could be imaged.

There are some limitations to the GPR method as well. Stott (1996) found that his GPR system exaggerated vertical tunnel height by a factor of 1.43. In this study tunnel height could not be determined as the reflection derived from the top of the burrow in most cases was so high in amplitude that it effectively interfered with any reflections that might have occurred from the burrow base. In addition, the suitability of GPR to survey animal burrows in media other than dry sand can not be predicted. While sand is well known as excellent for radar transmission, silty and clay-rich soils would likely attenuate energy prior to reaching the depth of burrows. For most intermediate-sized burrowing vertebrates that inhabit dry upland sandy regions of Florida, however, this would not be a problem. There have also been no tests of this technique with smaller (e.g., rodent) sized burrows. Burrows I surveyed were

approximately 25-35 cm in width and 11-18 cm high. My burrow camera showed the existence of smaller Florida mice (Podomys floridanus) burrows intersecting the main tortoise tunnels, but the GPR profiles did not discern these smaller tunnels. It is possible that antennae with very high frequencies (greater than 900 MHz) could potentially be used to image smaller burrows, following techniques discussed in this paper. Higher frequency antennae have a greater resolution, but a shallower depth of total energy penetration. Finally, I was unable to confirm the presence of tortoises in two burrows where the camera showed that they were in fact there.

In this study, a catalog of the shape, depth and orientation of burrows was produced for 14 gopher tortoise burrows in central Florida. Data were collected in dense grids of reflection profiles over 8 field days, which were then interpreted to show their orientation in three-dimensions. I demonstrated that the GPR method can be accurately and cost-effectively used in these types of studies for not only for burrowing reptiles such as gopher tortoises, but potentially many other burrowing organisms. This imaging technique potentially has worldwide conservation implications for the study of these structures and the medium to large-sized vertebrates that dig and use them.

Table 5-1. Data for gopher tortoise burrow study collected without and with ground penetrating radar.

Data gathered before use of GPR				Additional data gathered with GPR			
Burrow Number	Habitat	Length (m) probed	Tortoise Present ?	Beginning Direction	Ending Direction	Configuration	Maximum Depth (m)
NE1	Scrub	4.9	N	160 °	? ^b	turned left	2.48
NE2	Scrub	2.1 ^a	N?	260 °	? ^c	straight	1.28
Nor1	Scrub	4.1 ^b	Y	330 °	225 °	turned left	1.76
Nor2	Scrub	5.9 ^b	Y	170 °	55 °	turned left	1.52
Nor3	Scrub	3.4	Y	215 °	105 °	turned left	1.84
Nor4	Scrub	5.9	Y	315 °	30 °	turned right	2.88
KerrA	Sandhill	>7.6 ^c	?	60 °	75 °	straight	1.92
Kerr1	Sandhill	> 7.9 ^c	?	310 °	210 °	turned left	1.04
Kerr2	Sandhill	> 7.9 ^c	?	295 °	190 °	turned left	3.68
Kerr3	Sandhill	3.6 ^b	Y	200 °	? ^b	turned left	2.0
Kerr4	Sandhill	6.7 ^b	Y	320 °	125 °	turned right	3.2
Kerr5	Sandhill	5.8	N	40 °	230 °	turned left	1.92
Kerr6	Sandhill	> 6.4	N	240 °	120 °	turned left	1.52
Kerr7	Sandhill	6.1	N	10 °	230 °	turned right	2.24

^a Unable to manipulate camera past this point in burrow

^b Gopher tortoise at length indicated, unable to manipulate camera past tortoise, burrow continues unknown length

^c Burrow extends beyond length of camera; gopher tortoise probably residing in burrow based on recent tracks and sign



Figure 5-1. Pulling GPR antenna in perpendicular direction across the long axis of a gopher tortoise burrow in a sandhills plant community, Ocala National Forest, FL. Note mound of sand behind antenna, indicating where tortoise piled up sand from digging activities.



Figure 5-2. Two dimensional profile of burrow Kerr6 on ground surface. The path of the burrow is outlined by the line marked by flags and spray paint, with the tube of the video camera also aligned along the path. View is opposite to the digging direction of the tortoise, with the burrow opening at the upper center of photo.

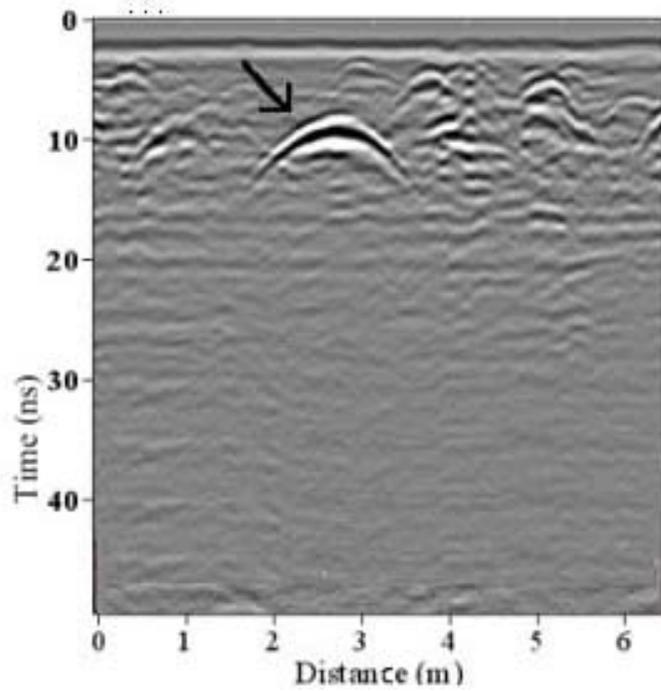


Figure 5-3. Hyperbole (indicated by arrow) shown in GPR reflection profile, collected by moving the GPR antenna on the ground surface over the burrow at a 90 degree angle to the orientation of the burrow.

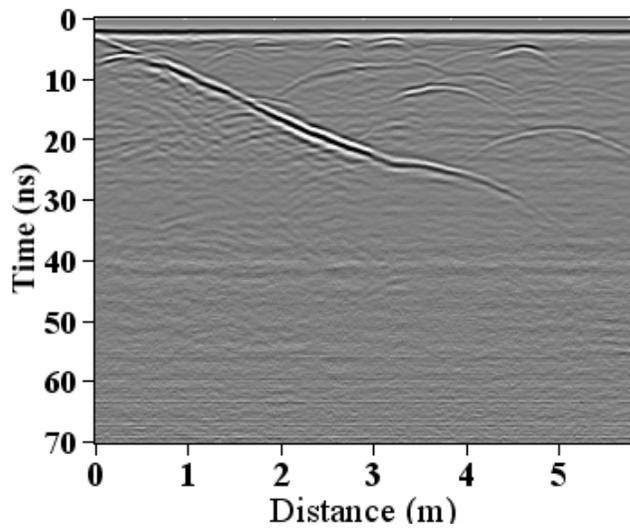


Figure 5-4. GPR longitudinal profile of burrow, collected by moving the GPR antenna on the ground surface following the path of the burrow.

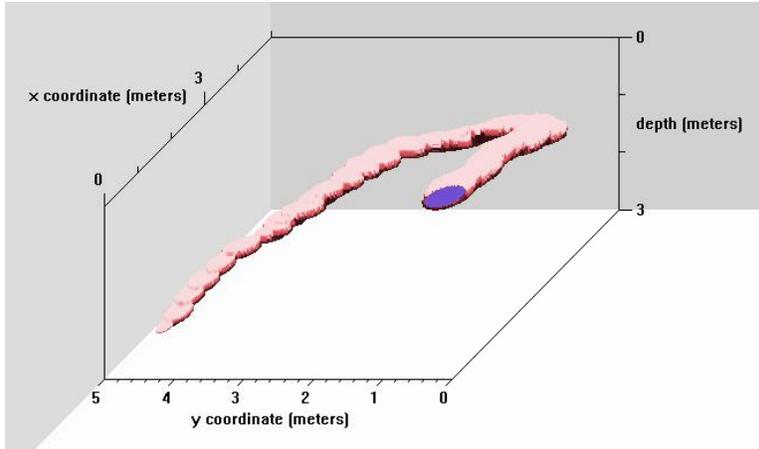


Figure 5-5. Three dimensional image of burrow Kerr3 developed using the Slicer-Dicer isosurface modeling program.

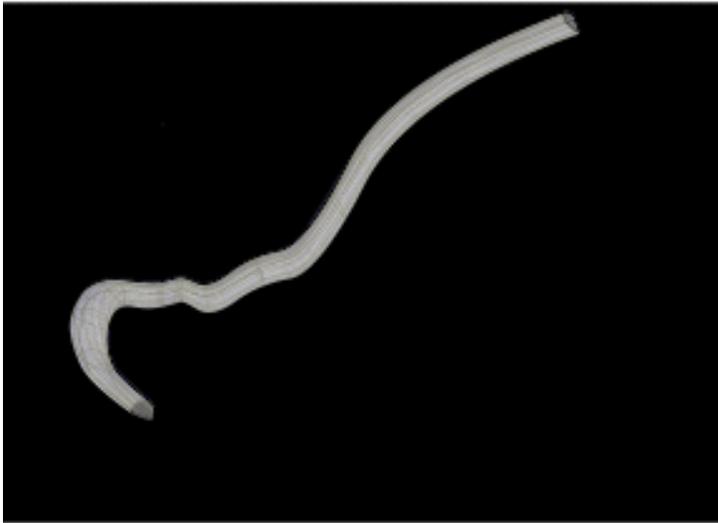


Figure 5-6. Black on white three dimensional rendering of burrow Kerr6 developed with the FormZ program.

CHAPTER 6
BIOLOGICAL APPLICATIONS OF FULL RESOLUTION 3D
GROUND PENETRATING RADAR IMAGING

Introduction

In Chapter 3, I outlined how ground penetrating radar can be applied to image gopher tortoise burrows. The methodology used in that study is referred to as “2D” GPR. A “full-resolution 3D” methodology has recently been developed (Grasmueck et al. 2005) which can delineate the internal architecture of the subsurface objects immediately underneath the ground surface with much more clarity than 2D GPR imaging. This method requires “very dense” survey grids, the distance between each survey transect being equal to a quarter of a wavelength. This full resolution imaging requires unaliased recording of reflections and diffractions coupled with 3D migration processing (Grasmueck et al. 2005). In this chapter, I do not discuss the geophysics involved, but present images of four tortoise burrows from the Kerr site that were examined using this technology. I then discuss possible biological applications.

Methods

In January, 2006, I joined a field crew from the RSMAS Marine Geology and Geophysics Laboratory of the University of Miami, led by Dr. Mark Grasmueck, who came specifically to survey burrows at my Kerr study site . We imaged four burrows: Kerr1, Kerr2, Kerr3, and Kerr4 using seven surveys. Two different frequencies were used for Kerr4: a 250MHz antenna with a 10x5 cm 3D grid, followed by a 500 MHz antenna with a 5 x 5 cm 3D grid. Additionally, for Kerr1, two different directions were used (Fig. 6-1).

Results

After the data were processed, video animations were prepared. Still images from these animations are presented in Figures 6-2 through 6-5. Although these images were similar to the 2D images (chapter 5), they had a better resolution. In these four Figures, the turquoise colored spiral is the tortoise burrow and the pink rings circling the tortoise burrow are almost surely burrows of the Florida mouse. The dark blue areas represent old tortoise burrows, or at least larger air voids occurring in the underground.

Discussion

One application of full resolution GPR is that it allows us to confirm or deny underground features examined by previous techniques. The dramatic images in Figures 6-2 through 6-5 confirm the findings of Jones and Franz (1990), who described five tortoise burrows by time consuming excavations. Two of their burrows showed a curve in the main tunnel. At the Kerr site, three of the burrows curved (Figures 6-2, 6-3, and 6-4) and one was fairly straight after two small initial turns (Figure 6-5).

This technology can clarify or sharpen our understanding of underground features. All the burrows imaged in this study included side burrows. If I am correct in my interpretation that these side burrows (pink areas in Figures 6-2 through 6-5) are burrows of the Florida Mouse, this confirms reports in the literature [Layne and Jackson (1994); Eisenberg (1983)] describing a close relationship of this rodent with the tortoise burrows. In this case, the 3D radar allowed us to catalogue the number of these side burrows; Kerr1 alone had seven (Table 6-1).

Another application of this technology is that it allows us to discover new information about features that have been suspected by natural historians to exist, but not proven. The

large number of “blue” areas in the images indicate that parts of old tortoise burrows remain intact underground long after the entrance is filled in and not even distinguishable as an old burrow entrance. In the 2D radar profiles I collected in scrub, I saw a number of hyperboles in the survey plots that were not part of the burrow I was tracking. Those hyperboles represented old burrows; in a few cases I could distinguish the remains of an old entrance near the location of several of these hyperboles. Based on several years of research sampling gopher tortoise burrows with a vacuum, J. Butler (Entomology Department, University of Florida) believes that the main tunnel of tortoise burrows can remain intact after the entrance is filled in with soil and debris, perhaps for decades (pers comm.). He suggests that these underground reservoirs may be important refuges for ticks. In his study of Florida mice, Newman (1997) reported small openings the size of a mouse at former tortoise burrow openings (he referred to them as “gone” burrows) and recorded mice escaping into those holes at some sites where he released them after capture. Moreover, I have observed a number of these rodent sized holes at abandoned (and filled-in) tortoise burrows at several of my six study areas in central Florida (described in Chapter 7). The GPR confirms that these underground chambers are intact; my observations along with those of Newman (1997) confirm that these chambers are biologically important.

When one considers the large number of both relict and new burrows of the tortoise, along with the large number of tunnels dug by the completely fossorial pocket gopher (*Geomys pinetis*) and other semi-fossorial burrowing rodents (e.g., *Peromyscus polionotus*), the soil landscape of some scrub or sandhill areas in Florida may resemble a sponge-like or honeycomb structure with numerous cavities. This architecture may have important ecological and evolutionary ramifications for true fossorial (e.g., *Neoseps reynoldsi*) and

semi-fossorial (e.g., Pituophis melanoleucus) species that regularly reside in these habitats. So an important application of this technology is that it allows us to quantify this practically unknown aspect of the landscape.

The accurate measurement of the dimensions of the burrows is fundamental to understanding the geometry of the burrows. Good measurements of the length, depth, angle of descent, and curvature of the burrows were obtained (Table 6-1). The average depth of the four Kerr burrows was 4.2 meters; average length was 10.7 meters. Additionally, the very dense 3D grid was able to correct small errors in the path of burrow Kerr2 that were predicted by the 2D GPR (Figure 6-6). One burrow was oriented in a northern direction, one in a southern direction, and two faced eastward (Figure 6-7).

The greatest advances in diagnostic medicine occurred when imaging methods became available that showed internal organs of the body. Understanding and treatment often depends on knowing if disease processes have eroded an organ or caused it's location to shift in relation to other parts of the internal anatomy. Looking at these full resolution 3D images is analogous to showing the medical doctor the first CAT scan some 20 years ago. This technology should help us make great advances in understanding burrow systems of semi-fossorial and fossorial vertebrates. These virtual 3D images should clarify the location of food chambers, escape tunnels, and help us comprehend the overall complexity of the burrow. The information and images in this chapter are new, since this was the first application of this technique to animal burrows. The tremendous potential of full resolution 3D GPR to understanding the subterranean world is only beginning to be appreciated.

Table 6-1. Statistics on 4 Gopher Tortoise burrows at the Kerr sandhill site, determined by 3D ground penetrating radar. See text for details.

Burrow	Length (m)	Maximum depth (m)	Angle of descent	Direction	Number of Florida Mouse burrows	Number of relict Tortoise burrows in plot	Number of root segments	Depth interval of tree roots (m)
Kerr1	11.77	4.60	23.0 °	turns left	7	1	9	0.72-1.42
Kerr2	12.52	4.62	21.7 °	turns left	1	7	19	0.48-1.24
Kerr3	9.92	4.15	24.7 °	turns right	5	7	10	0.95-1.36
Kerr4	8.42	3.37	23.6 °	straight	5	8	10	0.91-1.89

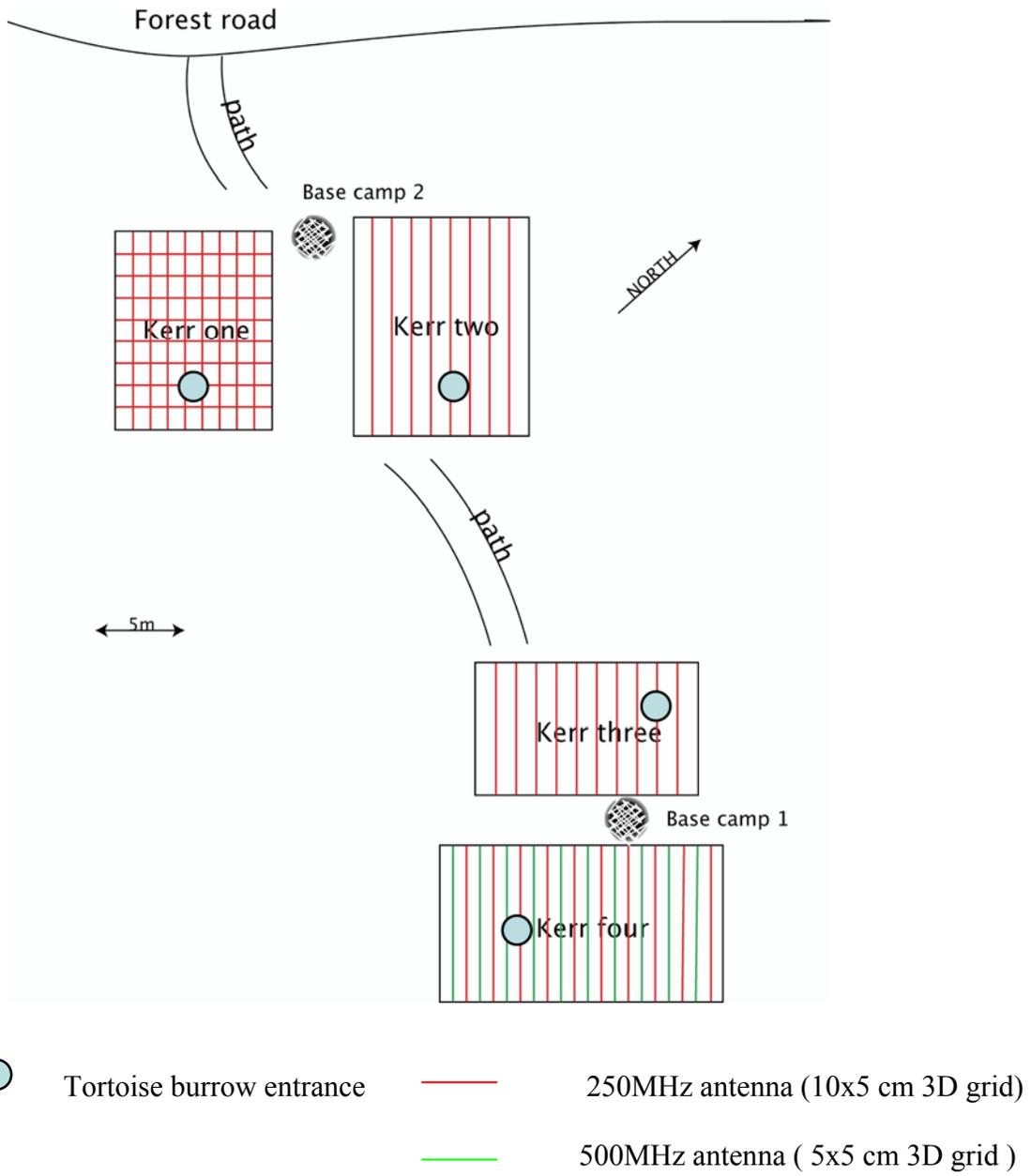


Figure 6-1. Survey plan for 3D GPR surveys in January, 2006, at Kerr site, Ocala National Forest. See text for details.

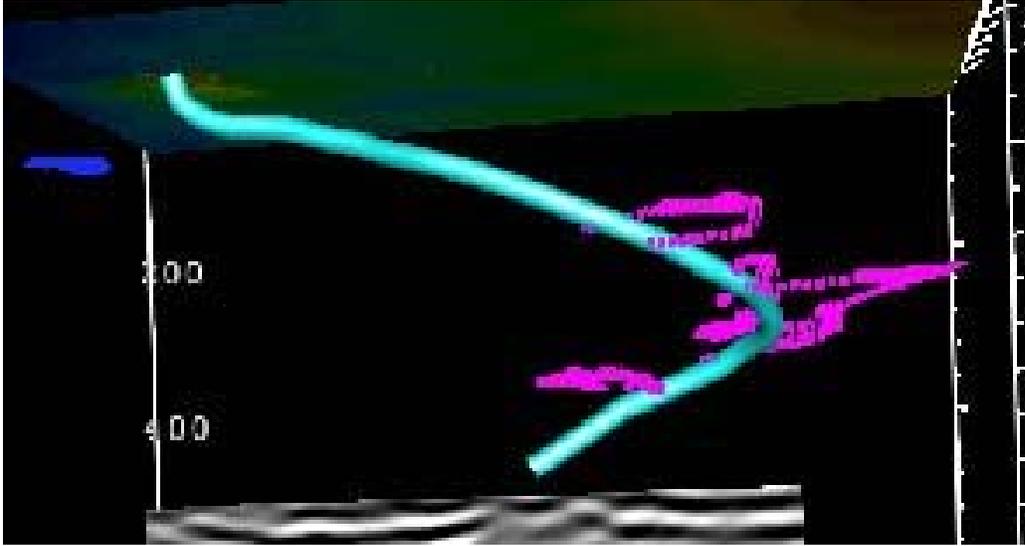


Figure 6-2. Three dimensional image of burrow Kerr1. Large curving light blue tube is the tortoise burrow. Pink rings circling the blue tube are assumed to be Florida mice burrows. Dark blue image on left side of screen is an old burrow.

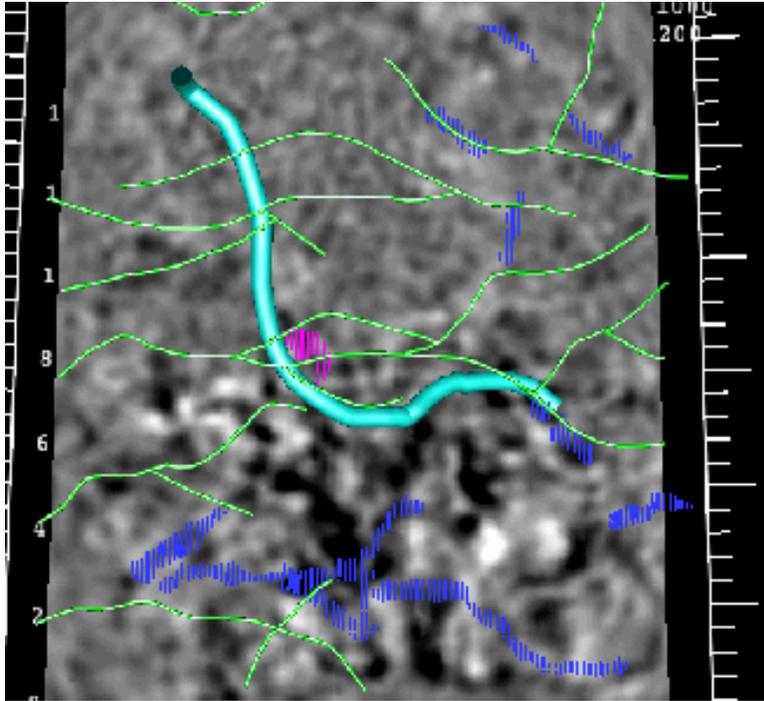


Figure 6-3. Three dimensional image of burrow Kerr2. Large curving light blue tube is the tortoise burrow. Pink rings circling the blue tube are assumed to be Florida mice burrows. Dark blue images on lower part of screen are old burrows. This view is looking down on the burrow from the ground surface. Green lines are tree roots. Entrance to the burrow is towards the top of the figure.

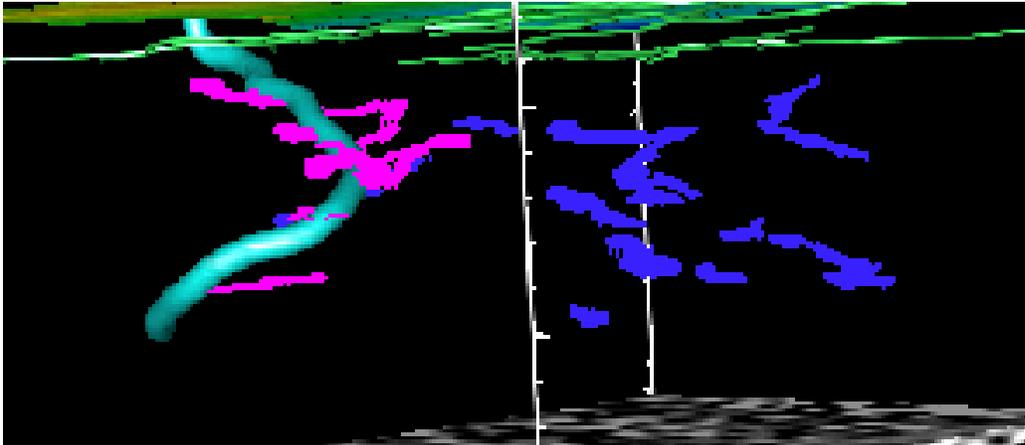


Figure 6-4. Three dimensional image of burrow Kerr3. Large curving light blue tube (left side of screen) is the tortoise burrow. Pink rings circling the blue tube are assumed to be Florida mice burrows. Dark blue images on right side of screen are old burrows. In this image the burrow enters the ground on the left side, then appears to make two small twisting turns, then makes a large spiral.

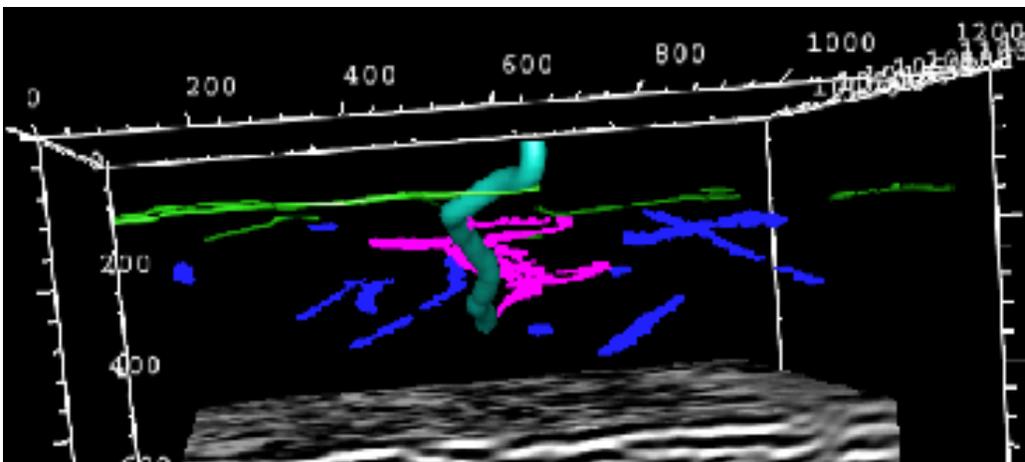


Figure 6-5. Three dimensional image of burrow Kerr4. Large curving light blue tube is the tortoise burrow. Pink rings circling the blue tube are assumed to be Florida mice burrows. Dark blue images are old burrows. On this image the burrow is moving away from the observer.

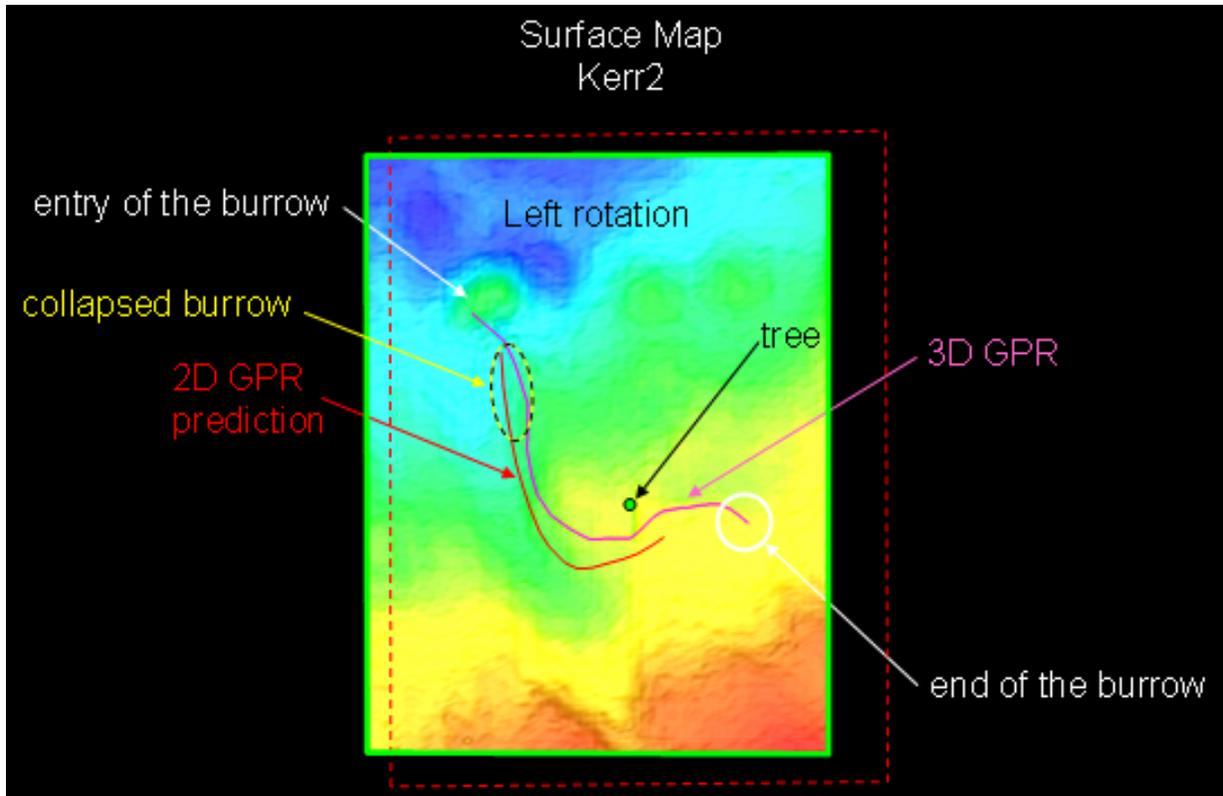


Figure 6-6. Validity of 3D GPR imaging over 2D GPR at burrow Kerr2. The 3D radar was able to discriminate the section of old burrow near the entrance that the 2D radar could not, and the path of the burrow is corrected with the 3D technology.

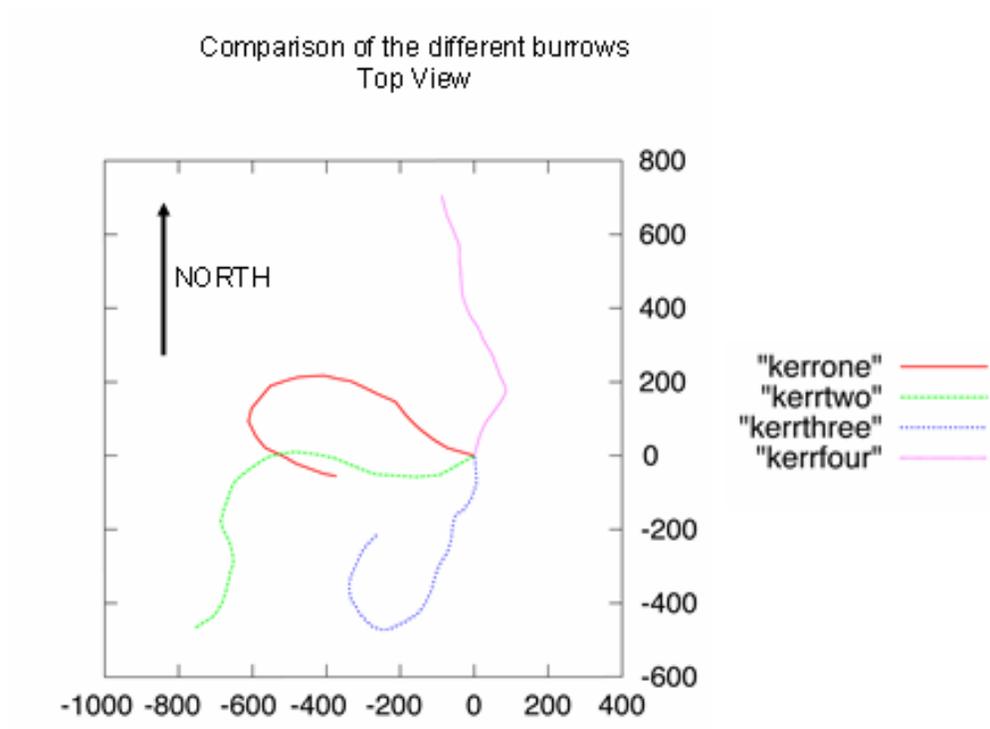


Figure 6-7. Comparison of 4 Kerr burrows, top view (looking down into the ground). Scale is centimeters.

CHAPTER 7
OCCUPANCY OF FAUNA INHABITING GOPHER TORTOISE BURROWS
LOCATED IN SCRUB AND SANDHILL VEGETATION OF CENTRAL FLORIDA

Introduction

Nichols et al. (1998b) proposed a method to compute species richness, along with colonization and extinction coefficients from data collected repeatedly at sites. Available literature suggests that a surprisingly rich fauna inhabits burrows of vertebrate excavators (Table 2-1), I recognized that burrows might be “miniature” systems to sample and compute these metrics, with the ultimate aim of testing ideas in biogeography on a small but tractable scale. In Florida, there are reports of at least 352 species of vertebrates and invertebrates using burrows of the gopher tortoise (Burke and Cox, 1988), so I chose the burrows of this species as a model to sample and attempt to compute these metrics.

The richness approach discussed above is based on capture-recapture theory and has been recently extended by Nichols and his colleagues (MacKenzie et al.2006) to estimate site occupancy by species at such re-visited sites. Because two threatened species, the Florida mouse (*Podomys floridanus*) and the gopher frog (*Rana capito*), are frequent inhabitants of the burrows of the gopher tortoise (Newman 1997, Godley 1992), a secondary goal for this study was to attempt to estimate occupancy of these species in the burrows, using program PRESENCE from Patuxent Wildlife Research Center, Laurel, MD. This program accepts data in the form of a matrix, with individual rows representing the sites and columns representing the occasions each site was visited by the researcher. The data in each row consists of zeros and one's, zero indicating that the species was not detected at that site on that occasion, and a one indicating that the species was detected. The program computes estimates of occupancy (“psi”), detection probability (“p”), and their standard errors.

Tortoises dig burrows in upland habitats with sandy soil, seeming to prefer sites that have a fresh growth of herbaceous vegetation, especially after recent fires (Diemer 1992). Although they seem to prefer sites with deep sand, they will dig burrows at sites with shallower sand, and will chose sites with thick root mat (e.g., Kennedy Space Center) if other sites are not available. Since Myers (1990) had suggested that scrub sites might support several thousand species of arthropods and the species richness of high pine plant communities is known to be very diverse, the pieces were in place to conduct a study of the burrow inhabitants under a variety of environmental conditions.

Study Areas

Gopher tortoises use a variety of upland habitats in Florida, but good densities are found in the scrub and sandhill plant communities (Diemer 1992), so I chose these two habitats as treatments. I chose three replications per habitat. For the three sandhill replications, I chose study tracts in the Ocala National Forest (ONF), Wekiwa Springs State Park (WSSP), and the Walk-in-the-Waters tract (WALK) of Lake Wales Ridge State Forest. For the three scrub replications, I chose early successional stands of scrub in the Ocala National Forest, the Arbuckle tract of Lake Wales Ridge State Forest, and Kennedy Space Center. The soil types for the scrub and sandhill areas are described in Chapter 5 (Astatula sand (AsB) for the scrub and Astutula (AtB) for the sandhill plots). The sandhills study plots at WSSP was Candler fine sand and the sandhills plots at the WALK study tract was Astatula sand also. The soil on my study plots at the Arbuckle scrub was Satelite sand, and the KSC soil were classified by Schmalzer et al. 2001 as coquina scrub soil. To randomly pick the sandhill plots, first a clear acetate sheet was overlaid over each study tract. The acetate had numbered squares drawn, each of which was scaled to equal 1 km² on the underlying GIS

map. Using a random numbers table (Steel and Torrie 1980), I selected eight sites from ONF, four sites from WALK, and six from WS. At each site, the 1 km² square was usually further subdivided into 5-hectare squares, except at WSSP, where only 1-hectare plots were chosen. Using the random selection procedure just described worked for the sandhill communities because generally these are large and contiguous in each Forest/Park. For the scrub plots, this random selection procedure was simply not possible. At ONF, preliminary observations by myself and ONF natural resources staff indicated that the tortoises prefer sites with vegetation that has grown to about one to two meters after a forestry clear-cut. They seem to avoid the fully grown stands of Sand Pine. Basically I had to choose sites from stands that were available. I did not have the option of choosing random sites from a large area. Similarly, at Arbuckle, there were only certain scrub areas that had been cut or burned and contained tortoises. At KSC, the scrub around the Happy Creek area is larger. Using a GIS map of the plant communities, I chose sites in a quasi-random fashion along access roads. This selection procedure may have introduced some bias.

Sampling Methods

In the first phase of this project, I attempted to sample 60 burrows at each of the six sites using six different methods (10 burrows/method): open bucket trap, funnel trap, sticky trap, Sherman live trap, video camera probe and vacuuming (Figure 7-1). It became apparent early that this procedure was logistically difficult for several reasons. Just the preliminary step of locating 60 burrows in the low density scrub sites was sometimes not possible. Moreover, the funnel traps were highly inefficient, capturing only a few species.

It became clear that I needed a new conceptual model of what it was I was sampling. I used the metaphor of the burrow as an airport. At many airports people fly in, drive in, or

arrive in via the underground subway. Similarly, individual animals move into the burrow by flying, crawling/hopping, or perhaps by burrowing through the soil or using the underground tunnels illustrated by our ground penetrating radar images. With this in mind, I developed a combination trap (Figure 7-2). This consisted of a five gallon bucket with a sleeve placed in the side which fits a short distance down the burrow. The floor of the sleeve was covered with sand from the burrow, and led to a second five gallon bucket arranged as a pitfall trap at the mouth of the burrow. Placed on top of the center part of the trap is a Malaise trap. The Malaise trap consists of three parts. A large “melon tub” (available at the produce department in grocery stores) was flipped upside down and a hole cut into the top. A 32 oz. clear plastic beverage container (with the bottom cut out) was glued to the ring around the hole of the melon tub. A clear plastic canister was then glued on top of the beverage container, with a few ounces of antifreeze contained in a small saucer placed inside the canister. The canister served as the collection device for the insects. On day 1 during the second phase of this study, I placed the combination trap at each burrow to be sampled. On the second day, after collecting the captured individuals from the Malaise and pitfall traps, I removed the combination trap and then used a video probe camera to determine if a tortoise was actually residing in the burrow. I then vacuumed the burrow, following the method used by Milstrey (1987). At other burrows where I did not use the combination trap, I placed some sticky traps or used the vacuum. I also field-tested a small number of “stand alone” Malaise traps (Figure 7-3). I placed some small pan traps in the floor of some burrows, just behind the entrance (Figure 7-3). These traps were plastic containers about 10 cm wide, 24 cm long, and 4.5 cm deep. Finally, I used an additional method that was successful for sampling gopher frogs on rainy days. On days when rain was about to begin or had just started, I observed

gopher frogs exiting the burrows. I realized that if I timed my surveys correctly (just when the rain was about to begin or just as the rain started), I could observe and count the frogs as they sat in each burrow entrance, if I approached each burrow very quietly. Because this method is biased towards gopher frogs, I balanced the number of these observations by placing an equal number of Sherman traps (for Florida Mice). By using this series of methods, each aimed at capturing a different subset of burrow inhabitants, I believed I had the optimal procedure to sample the diversity of species residing in the burrows.

As time permitted, I collected the following environmental variables at each burrow: distance to nearest body of water, distance to nearest active burrow, density of burrows in area, height and width of burrow, “activity status” (active or inactive) of the burrow, and if a camera was used to examine the burrow, I included presence/absence of gopher tortoise in the burrow.

The combination trap only captured crawling or flying species that were exiting the burrow. Thus, towards the end of the project, I sampled some burrows with “open” buckets, which captures species that crawl/hop into (as well as out of) the burrow. I devised a flight interceptor trap (Fig.7-3) which captures species flying into or out of the burrow, but only a small number of these were tested.

All vertebrates that had adequate morphological features were identified to species. For invertebrates, I used a “rapid assessment” technique and only identified each species in the sample to order, class or family.

Following the field sampling procedure just outlined was very time-consuming and I was not able to sample a large number of burrows on any given day. Additionally, some of the burrows I had sampled on the previous visit had been abandoned by the tortoise, and in

some cases, were partially or completely dilapidated. Thus, it was problematic to follow the sampling guidelines necessary to compute species richness or occupancy on a burrow by burrow basis because many burrows did not exist on repeat visits. This decline in the number of sampled burrows caused a high number of missing values in the data matrix to be entered into the Presence program, resulting, at some point, in unreliable estimates. Thus, I changed my sampling universe, and re-defined the “site” as “the collective number of burrows on each visited plot” (rather than individual burrows). During the fieldwork, I had continued to collect data at previously sampled burrows, as well as new ones tortoises had dug in the same plot. By using all the sampled burrows in a plot as spatial replications (multiple visits) on the same plot, I was able to compute some occupancy estimates, with the inference being directed at “the species that occupy burrows on the selected plots”. I defined a short season (the 5 month period from July through November, 2005, the best dataset) so that it was unlikely that the true occupancy parameter I was estimating actually changed during the data collection period.

Results

I collected 1502 samples from the six study tracts around Central Florida from 2000-2005, primarily using pitfall traps, Malaise traps, and by vacuuming (Figure 7-4). The samples consisted of 24 families and orders of invertebrates which were captured and preserved, along with 18 species of vertebrates which were captured, weighted, and released, or observed (without capture) at the burrow (Figure 7-5 through 7-8, Table 7-1). Although identification to genus and species was not done for many invertebrates, when I considered the number of different species I had observed during the data work-up (especially beetles,

ants, flies, and moths), I estimated a species richness of between 60- 70 species using the burrows I sampled.

In the ONF, many more gopher frogs were captured in sandhill than in scrub, but only a few more Florida Mice were captured in sandhill over scrub (Figure 7-6). The best model chosen by the Presence model selection procedure estimated that gopher frogs occupied over three times as many plots in the sandhills over scrub plots (Table 7-2). These occupancy estimates are reversed for the Florida mouse, with about twice the percentage of scrub plots being occupied over sandhill (Table 7-2).

The Presence program consistently chose models for both species with a constant occupancy parameter (ψ) and a constant detection probability (p) (Table 7-3). Both the probability of both species occupying a burrow together and the probability of detecting both species, given that they were both present in the burrow, was higher in the sandhills than the scrub (Table 7-4)

There were enough captured ticks (all species combined) in individual burrows at the Kerr sandhill plot for the data to be analyzed with Presence (Table 7-5). When analyzed as is, the data comprised a 23 by 19 matrix (437 values), with 314 missing values. The estimated ψ was 0.81 (SE 1.3). When the data for each month was combined into one value (either a 1 or a 0), the 23 by 4 matrix (no samples in August) contained 18 missing observations, and the program estimated an occupancy of 0.76 (SE 0.16).

Discussion

My species richness estimate is similar to that of Knizley's (1997), who captured a total of 56 species in gopher tortoise burrows at a site in Alachua County. She also sampled the burrows for both vertebrates and invertebrates using multiple methods.

The model estimates of occupancy for the gopher frog agree with the account by Godley (1992) who suggested that densest populations of this anuran occur in the longleaf pine-turkey oak sandhill association. Similarly, model estimates for the Florida Mouse agree with Layne (1992) who believed that the scrub community is much closer to the ancestral habitat of Florida Mice rather than sandhill. There are accounts in the literature indicating that both species show a high fidelity to gopher tortoise burrows, so my assumption that the real parameter ψ did not change during the study period was warranted.

The fact that the program chose models with constant detection over models with varying detection probabilities is consistent with the biology of these species. By living in an enclosed burrow, the frogs and mice may be somewhat insulated from fluctuating environmental conditions and may appear at the surface of the burrow in a somewhat regular fashion. In Table 7-3, I list the first two competing models for each species-habitat combination. Using the commonly recognized criteria for AIC model selection of choosing models with an AIC difference of less than two (Burnham and Anderson 2002), in three cases one model was clearly better. For Florida Mice in the scrub, there was an AIC difference of 1.67 between a model with one group with constant ψ and p over a model with two groups, each with a different (but constant) p . In that case, I computed the model average value for ψ of 0.73. There was some support (Δ AIC) for a model for Florida Mice in the sandhills with detection probability that varied over time. However, that model had 15 parameters, whereas the model with one group with a constant p had only two parameters and was likely the best model in that case. Using this same reasoning based on parsimony, I listed what is likely the “best” model first for gopher frogs in Table 7-3.

The Kerr plot where much of the sandhill data was collected was adjacent to a breeding pond that gopher frogs likely used. This probably explains the very high occupancy value for this species. The scrub plots I sampled were more fragmented, having large areas of older growth sand pine stands and fewer ponds for breeding. It would likely be difficult for gopher frogs to achieve a population density (and occupancy status) in the ONF scrub even close to that in the sandhills.

With the tick data, one would expect a high value for burrow occupancy of this blood parasite. The model predicted about a 20% higher occupancy in the burrows than the naïve estimate, a considerable difference.

In species richness and occupancy studies, different methods may be positively or negatively biased as far as capturing certain species. Thus, “method bias” should be considered when interpreting the results. With the captures of frogs and mice, I tried to avoid this by balancing the OBS attempts with the Sherman attempts, since each method is selective for each species. However, the primary method used in this study to capture vertebrates was the bucket trap. I suspect that Gopher frogs may be more vulnerable to capture by this method than Florida Mice. This may be reflected in the co-occupancy statistics: the probability of detecting gopher frogs in the scrub was much higher than the probability of detecting Florida Mice (0.57 versus 0.18, given both present, Table 7-4), even though overall occupancy by Florida Mice in the scrub was higher than that of gopher frogs (0.65 versus 0.25).

Different ecological communities in Florida are tied to the soil types in which they occur. In a “micro” sense, this is probably true for the communities of species occurring in burrows. In Chapter 2, I briefly discussed the effects of the soil on burrow architecture and

species distribution. Future research should examine the functional relationships that likely exist between the distribution, density and architecture of burrows and the underlying soil type. Our GPR results indicated that tortoises can dig burrows to considerable depths in well drained sandy soils with a deep water table. I did not conduct any GPR surveys at the Arbuckle or KSC scrub, where the water table is higher, but my depth probes showed that the burrows were much shorter. On occasions, I could see standing water in the burrows at a depth of about one meter. Most of the burrows in this study were in areas with fine sand. Fine sand may be more easily compacted by the tortoise's sideways digging motion, aided by the scraping action of the carapace against the top of the tunnel. The integrity and durability of the burrow is probably closely tied to the morphology of the soil.

The ephemeral nature of gopher tortoise and many vertebrate burrows present a challenge to researchers attempting to measure the biodiversity residing in these structures. In this study, perhaps a better strategy would have been to select fewer plots and visit those more often, using unobtrusive sampling methods for vertebrates, such as camera traps.

Table 7-1. Number of occasions that all vertebrates seen in the study were captured or observed at the burrow entrance or at a matching bucket trap in the burrow study.

Genus or Species	Common name	Number of Occasions	Captured (C) or Observed (O)
<u>Rana capito</u>	Gopher frog	122	C, O
<u>Podomys floridanus</u>	Florida mouse	37	C
<u>Peromyscus polionotus</u>	Old Field Mouse	6	C
<u>Peromyscus gossypinus</u>	Cotton Mouse	11	C
<u>Sigmodon hispidus</u>	Cotton Rat	3	C
<u>Gastrophryne carolinensis</u>	Narrowmouth Toad	12	C
<u>Bufo terrestris</u>	Southern Toad	7	C
<u>Bufo quercicus</u>	Oak Toad	2	C
<u>Sceloporus woodi</u>	Scrub Lizard	5	C
<u>Cnemidophorus sexlineatus</u>	Six lined race runner	2	C
<u>Tantilla relict</u>	Florida crowned snake	3	C
<u>Sistrurus miliarius</u>	Pygmy rattler	1	O
<u>Masticophis flagellum</u>	Coachwhip	4	O
<u>Pituophis melanoleucus</u>	Pine snake	1	O
<u>Blarina sp.</u>	Short-tailed Shrew	1	C
<u>Sylvilagus floridanus</u>	Eastern cottontail	1	C
<u>Coluber constrictor</u>	Black racer	>3	O

Table 7-2. Naïve and model estimates of occupancy (ψ) and detection probability (p) computed with program Presence for Gopher Frogs and Florida Mice inhabiting Gopher Tortoise burrows in the scrub and sandhill communities of Central Florida during July-November, 2005.

	Occupancy (ψ)			Detection probability	
	Naive	Model	SE (ψ)	p estimate	SE of p
Gopher Frog					
Sandhills	0.91	0.91	0.09	0.85	0.06
Scrub	0.25	0.25	0.15	0.47	0.12
Florida Mice					
Sandhills	0.27	0.30	0.15	0.25	0.09
Scrub	0.63	0.66	0.18	0.31	0.08

Table 7-3. Summary of models fit to Gopher Frog and Florida Mice occupancy data collected at Gopher Tortoise burrows during July-November, 2005.
 Legend: Δ AIC: differences in Akaike Information Criterion values for each model; AIC wgt: the model weight, or the probability that the model is the “best” model in set of models

	Model	Δ AIC	AIC wgt	Model Likelihood	NPar	Ψ
Gopher Frog						
Sandhill	Ψ (.) p (.) 2 groups	0.00	0.877	0.769	4	0.915
	Ψ (.) p (.) 3 groups	4.00	0.119	0.104	6	0.915
Scrub	Ψ (.) p (.) 1 group	0.00	0.869	0.756	2	0.253
	Ψ (.) p (.) 2 groups	4.00	0.118	0.102	4	0.256
Florida Mice						
Sandhill	Ψ (.) p (.) 1 group	0.00	0.775	0.60	2	0.305
	Ψ (.) p (t)	3.97	0.106	0.082	15	0.273
Scrub	Ψ (.) p (.) 1 group	0.00	0.685	0.469	2	0.663
	Ψ (.) p (.) 2 groups	1.67	0.297	0.204	4	0.939
				Model average		0.73

Table 7-4. Occupancy and detection probabilities for Gopher Frogs and Florida Mice co-occurring in Gopher Tortoise burrows in scrub and sandhill communities of Central Florida during July-November, 2005. Legend: prob = probability; Psi= estimate of occupancy; GF= Gopher Frog; FM = Florida Mice

Occupancy probabilities	Sandhill	Scrub
Psi by GF	0.91	0.25
Psi by FM	0.27	0.65
Psi by GF + FM	0.25	0.17
Detection Probabilities		
Prob detecting GF, FM not present	0.64	0.27
Prob detecting FM, GF not present	0.50	0.36
Prob detecting GF, given both present	0.50	0.57
Prob detecting FM, given both present	0.50	0.18
Prob detecting both, given both present	0.25	0.11

Table 7-5. Microsoft Excel spreadsheet of tick data for individual burrows from the Kerr plot for the 5 month period, July-November, 2005. A “1” in each cell indicates ticks were present in the sample on that date, a “0” indicates they were absent in the sample. Blank cells indicate that the burrow was not sampled on that date.

Burrow #	7/20/2005	7/28/2005	7/29/2005	9/20/2005	9/21/2005	9/27/2005	9/28/2005	9/29/2005	10/5/2005	10/6/2005	10/10/2005	10/11/2005	10/12/2005	10/15/2005	10/17/2005	11/6/2005	11/15/2005	11/16/2005	11/28/2005
6AA		1	0	0	0								0				0	0	0
BLFMB								0				0					0		0
J2000	0	0	0	0								0				0			0
J81		0	0	0			0				0			0					0
J82						0	0										0		
K11		1			1											0		0	0
K13								0										0	0
K2					1						0	0	1						0
K24		0			1											0		0	0
K27		0						0											
K3								1				0	1						
K6		0			0					0			1					0	
K7		1										0							0
Kerr1	0	0			0					0	1	1			0			0	
Kerr2	0				1			0					1					0	
Kerr3	0				1					0		0						0	0
Kerr4	0				0			1			0	1	1		1			0	0
Kerr5	0				1								0						0
Kerr6	0	0			0			0	0						0	0	0	0	0
Kerr7	1				1											0	0	0	
Kerr7B		0			0			0								0		0	0
KerrA	0				1		0	0										0	
old K6												0	0						0



A.



B.



C.



D.



E.



F.

Figure 7-1. Six trapping methods attempted early in study. A. open pitfall trap B. Funnel trap C. Sticky trap affixed to ceiling of burrow entrance D. Sherman trap being Slid into burrow E. video camera F. vacuum



A.



B.



C.



D.

Figure 7-2. Combination trap. A. Assembled, in side profile. B-D Assembly of combination trap. B. Step 1: open pitfall trap is set in ground in front of burrow opening. C. Step 2: center bucket is placed by sliding sleeve down burrow and fitting ring of center bucket on ring at top of pitfall bucket, and secured with duct tape. D. Step 3: the Malaise trap is placed on top of center bucket and secured with duct tape.



A.



B.



C.



D.

Figure 7-3. Malaise and experimental traps. A. "Stand alone" malaise trap, made with tomato cone B. "Stand alone" Malaise trap, made with cake lid. C. Flight Interceptor trap. A,B, and C set at burrow entrance D. Pan trap set in floor of burrow entrance

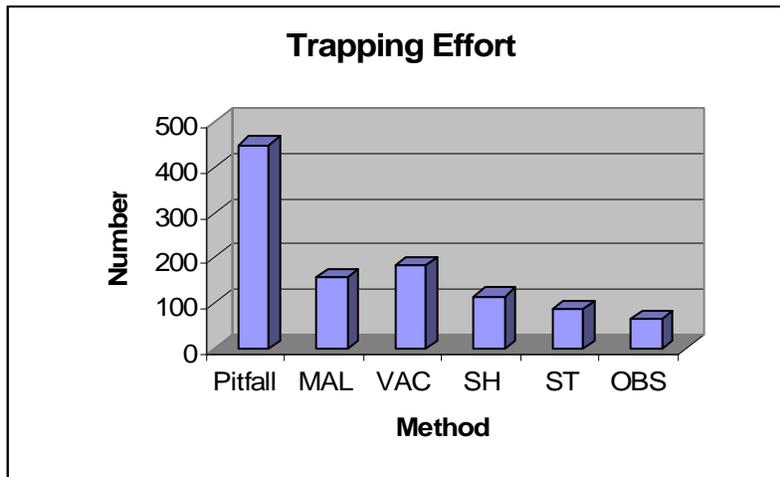


Figure 7-4. Overall trapping effort at burrow entrance, categorized by number of traps set per method. Legend: Pitfall: 5 gallon bucket traps; MAL: Malaise traps; VAC: vacuum; SH: Sherman live traps; ST: sticky traps set at roof of burrow entrance; OBS: observations at burrow entrance during rain events

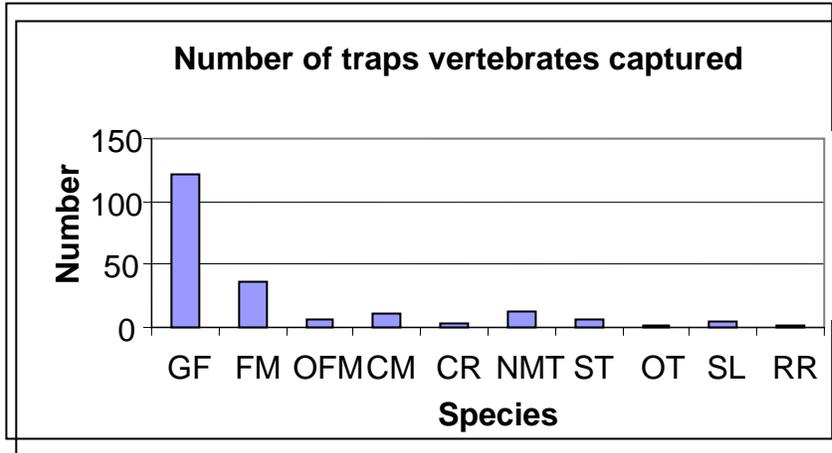


Figure 7-5. Number of traps in which vertebrates were caught at the burrow entrance with pitfall or Sherman traps or by observation.
 Legend: GF: gopher frog; FM: Florida mice; OFM: old field mice; CM: cotton mice; CR: cotton rat; NMT: narrow mouth toad; ST: southern toad; OT: oak toad; SL: scrub lizard; RR: race runner

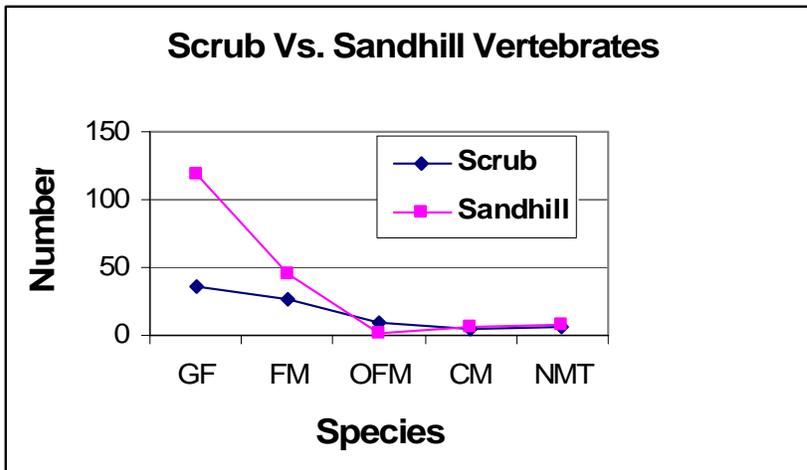


Figure 7-6. Comparison of the number of individual vertebrates captured at the entrance to Gopher Tortoise burrows in pitfall traps, Sherman traps, and by observation. Legend: GF: Gopher Frog; FM: Florida Mice; OFM: Old Field Mice; CM: Cotton Mice; NMT: Narrowmouth toads

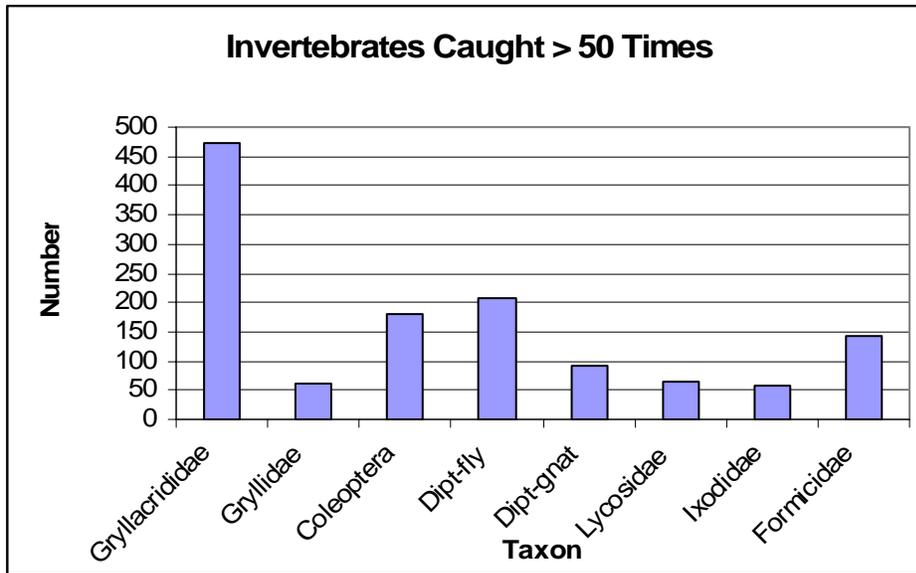


Figure 7-7. Invertebrates captured on more than 50 occasions during burrow study in scrub and sandhill communities in Central Florida.

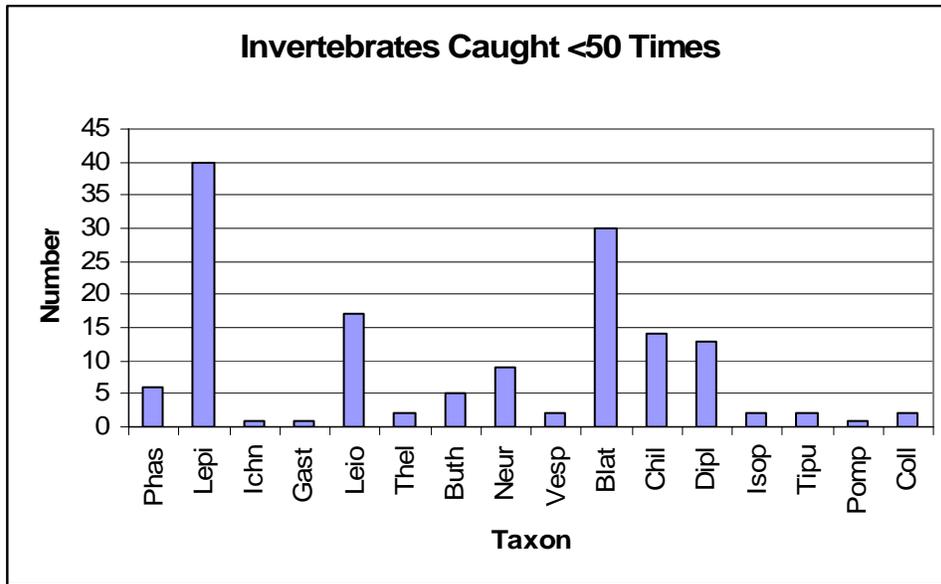


Figure 7-8. Invertebrates captured on less than 50 occasions during burrow study in scrub and sandhill communities in Central Florida. Legend: Phas: Phasmodea; Lepi: Lepidoptera; Ichn: Ichneumonidae; Gast: Gastropoda; Leio: Leiobunidae; Thel: Thelyphonidae; Buth: Buthidae; Neur: Neuroptera; Vesp: Vespina; Blat: Blattaria; Chil: Chilopoda; Dipl: Diplopoda; Isop: Isopoda; Tipu: Tipulidae; Pomp: Pompilidae; Coll: Collembola

CHAPTER 8
VERTEBRATE SPECIES RICHNESS AT AVON PARK AIR
FORCE RANGE, FLORIDA ESTIMATED WITH THE JACKKNIFE

Although all areas in southern Florida were studied in the wet summers and in the dry winters, it was not always possible to be at the right place at the right time. The element of chance figured strongly the night we first heard *Hyla gratiosa* in southern Florida.
Duellman and Schwartz 1958

Introduction: Species Richness Estimation

Florida has about 900 species of freshwater and land vertebrates and is one of the biologically richest states in the U.S. (Hipes et al. 2001). This natural diversity is at great risk, due to an unprecedented influx of people, which is fueling such development that it is completely obliterating many natural communities, overwhelming the natural resilience of remaining ecosystems, and either directly causing many local species extinctions and putting many other species on a trajectory towards extinction.

Species richness is often calculated from inventories of flora and fauna, which are conducted in environmental resource management for a variety of reasons. Often such diversity metrics are needed in environmental assessments or as part of an ecological risk analysis, to compare species richness in impacted versus non-impacted communities. Species richness is the most intuitive measure of community diversity, and “snapshots” of local richness provide data not only to understand current diversity but as a baseline to interpret future species declines due to human related causes.

Ecological inventories are usually presented as lists of species, usually compiled by field surveys, museum records, and prior reports. This approach of presenting the number of species observed is a necessary but crude first step in developing an unbiased vertebrate community profile at a site. Although field biologists understand that these lists represent a

sample of the faunal community, managers and policy makers often view these lists as a final statement about the faunal community when making conservation decisions. In comparisons of different species richness estimators, several investigators found that counts of observed species performed worse than all other methods (Brose 2002; Hellman and Fowler 1999; Walther and Morand 1998). Not only do such naive counts lead to a negative bias in richness estimates, they also confound any comparison between different areas, since typically they do not have any measurement of error associated with them (Nichols et al. 1998a).

Biology, however, is a probabilistic science. We measure the probability that an animal will be found at a certain site within its home range, or we make a population estimate with a confidence interval to realistically account for the error in our measurements. The same holds true for estimates of species richness. Thus, lists such as those discussed above are incomplete, because they simply represent a count of species observed, without taking into account the probability of detection or the error involved in obtaining the estimate (Nichols et al. 1998a). Some percentage of those species with lower detection probabilities are missed, resulting in a negatively biased richness estimator. Even with methods generally thought of as “certain” (e.g., electroshocking fish in a small portion of a stream), some species may escape detection for various reasons. Since most ecological communities have a number of rare species, and surveyors can never search every physical component of the habitat, all such searches are incomplete, and only a probabilistic statement is possible regarding the community composition (McArdle 1990). Often the very species that are missed due to low detectability are the ones most in need of urgent conservation measures.

Three approaches have been used to calculate species richness: 1) extrapolation of species accumulation curves; 2) fitting of species-abundance distribution; and 3) non-

parametric estimators, especially those used in capture-recapture methods. The first approach suffers from the same problem as counts; it is flawed because detection probability is not integrated into the calculations. The second method suffers from this same problem if the abundance estimates are calculated from counts of captured individuals, as they usually are. Some of these methods are also limited because they simply present an estimate without an associated variance. A substantial literature is emerging dealing with the issue of detectability in community ecology studies [Nichols et al. (1998a); MacKenzie et al. (2005, 2006); Williams et al. (2002); Pollock et al. (2002); Yoccoz et al. (2001)].

Non-parametric capture-recapture methods have traditionally been used in population trapping studies. These methods account for individuals missed because they allow for heterogeneity in capture probabilities. By analogy, these models have been shown to work equally well in the context of community ecology, to calculate number of species, because they allow for the number of species missed (Nichols et al. 1998a). This method not only provides an estimate with its associated error, along with relevant detection probabilities, but has been extended to multiple time points, making it possible to estimate local extinction, recolonization and turnover rates of species (Nichols et al. 1998b). The versatility of the capture-recapture approach is demonstrated by the fact that it is recognized as the gold standard in medicine to estimate “missed objects” (Lange et al. 2003) and demography (Cowan et al. 1986).

Of the different capture-recapture methods, the jackknife method of bias reduction (Gray and Shucany 1972) has performed consistently well in simulations involving both population studies (Otis et al. 1978, Burnham and Overton 1979) and species richness studies (Heltshe and Forrester 1983; Brose et al. 2003; Walther and Morand 1998). In particular, if

the range of sample coverage is from 0 to 86%, as most studies will be, the first to third order jackknife estimators have been shown in simulation studies to be the most accurate (Brose and Martinez 2004).

The species richness approach developed by Nichols et al. (1998a, 1998b, Hines et al. 1999) provide a flexible pathway for researchers to obtain more unbiased estimates of species richness in a faunal assemblage by accounting for detection probability. If sites can be re-visited, detection probabilities can be determined for individual species at each site, and this data analyzed using the COMDYN program (Hines et al. 1999). This approach was taken by Meyers and Pike (2006) to determine herpetofaunal diversity at the Alligator River Refuge in North Carolina. A second approach can be used if sites are not re-visited; relatively unbiased estimates of richness can be computed from a list of species using the jackknife estimator of Burnham and Overton (1978, 1979), as long as one sampling requirement is met and two assumptions are accepted. The sampling requirement is that investigators use a wide variety of methods so as to obtain a genuinely comprehensive and representative list of the assemblage as possible. This estimator is based on the seemingly weak assumptions that the N detection probabilities corresponding to the N different species in the community represent a random sample from some unspecified distribution (Nichols and Conroy 1996), and that the detection probabilities for each individual species remain the same on each sampling occasion. This second approach for computing species richness estimates is followed in this paper, using the state-of-the-art program SPECRICH (Hines et al. 1999). I compare species richness obtained from a simple count of vertebrates at a central Florida military installation with the richness statistic predicted by the SPECRICH jackknife estimator. The paper

discusses possible reasons species were missed, since this is an issue with species richness estimation that might not be fully appreciated by biologists.

Methods

Avon Park Air Force Range (APR) is a 42,927 hectare military installation located in Polk and Highlands counties, Florida. The major topographic feature is the “Bombing Range Ridge”, a north to south trending, sand ridge, 53.3 m. above sea level at the highest point, part of Florida’s relic system of dune ridges that comprised the Wicomico Shoreline during the early Pleistocene (Webb 1990). Three surveys have been conducted for vertebrates at APR from 1988 to 1998. Christman (1988) surveyed fauna residing in the APR scrub as part of a larger survey of Florida scrub. From May 1994 to October 1998, a second survey was conducted by Branch and Hokit (2000), who also restricted their survey to APR scrub patches, with a focus on scrub lizards (Sceloporus woodi), sand skinks (Neoseps reynoldsi), bluetail mole skinks (Eumeces egregius lividus), and gopher frogs (Rana capito aesopus; Table 8-1). A third survey was conducted from 1996-98 by a team of researchers, including the author, from the Florida Museum of Natural History to determine the distribution and abundance of seven sensitive vertebrate species occurring at APR in southcentral Florida (Franz et al. 1998). These seven species were Florida gopher frogs, gopher tortoise (Gopherus polyphemus), eastern indigo snake (Drymarchon corais couperi), eastern diamondback rattlesnake (Crotalis adamanteus), Florida mouse (Podomys floridanus), Florida roundtail muskrat (Neofiber alleni nigrescens), and Shermans’ fox squirrel (Sciurus niger shermani). Because of the wide range of ecological traits and habitats occupied by these seven species, most ecological communities were searched using a number of different survey techniques

(Table 8-1). Although birds or bats were excluded, many different vertebrates were observed during the surveys and all were recorded (Franz et al. 1998).

To determine if the published range maps of both recorded and “missed” species overlapped APR or not, I consulted the following standard references: a current, unpublished atlas of amphibian and reptile distribution maintained by K. Krysko at the Florida Museum of Natural History; Ashton and Ashton 1988a 1988b, 1991, Brown 1997, Conant and Collins 1991, Hips et al. 2001, Moler 1992, Humphrey 1992, and Whitaker, 1992.

Results

Franz et al. (1998) combined the results of their survey with the two earlier surveys mentioned above, resulting in a final tally of 94 different non-aerial mammals, reptiles and amphibians observed at APR using standard, repeatable survey techniques from 1988-98 (Table 8-2). The interpolated jackknife estimate of the number of species was 108 with a standard error of 5.3 species, indicating that between 9-19 vertebrate species were “missed”. Thirty-six species were identified as “candidate” species that could potentially occur at APR, based on their geographic range, biology, or the availability of suitable habitat at APR. Some of these “candidate” species may have been “missed” in our surveys.

Discussion

Four issues are critical in faunal inventories for species richness. These are: 1) true presence or absence; 2) detection probability; 3) availability; and 4) sampling method, intensity, and bias.

True Presence (True Positives)

Genuine presence or absence of a species is often very, very difficult to determine with certainty, even with standard methods. Constantly shifting distributional patterns of

vertebrates and seasonal metapopulation effects can dictate a species' occurrence at a particular site; thus, "true presences" or "true absences" recorded in the field can be transient categories, especially subject to change near the edge of a species' geographic range. I considered 93 of the 94 species listed in Table 8-1 as "true presences" or "true positives". Of those, 65 were recorded repeatedly, thus were very common.

False Positives

False positives could occur if the biologist reports an occurrence of a species in an area but the record is spurious. The most common reason for this in ecological inventories is taxonomic misidentification, e.g., the species or its sign is incorrectly identified. However, other reasons can occur: McLachlan and Clark (2004) list an example in a paleontological study in which pollen was blown into their study from a long distance away by high winds. At Avon Park, a false positive might have occurred with the single data point of the striped mud turtle shell found adjacent to a caracara nest. If the bird brought the turtle in from across the Kissimmee River (out of the area), this data point could reflect a false positive. We also viewed this record with some suspicion since there were no published records of this species at Avon Park.

True Negatives

A true negative would be the case in a survey if comprehensive surveys using an extensive variety methods specific for the species did not capture any species. There is a high likelihood that at least six of the 36 species in Table 6-3 were "true negatives". Branch and Hokit (2000) reported not finding the sand skink and the bluetail mole skink at Avon Park despite a tremendous four year multi-sampling effort specifically aimed at capturing them, but finding both species with little or no effort at the nearby Arbuckle scrub using the same

methods. The Southern Fence Lizard is common in pine flatwoods and longleaf pine-turkey oak habitats (Ashton and Ashton 1991) yet the extensive surveys for fox squirrels or tortoise burrows in similar upland habitats at APR conducted by the Franz team did not produce any observations. Sampling results also suggested that Spadefoot Toads (Scaphiopus holbrookii) probably do not occur at APR. This species estivates in shallow burrows in the ground during dry weather (Pearson 1955). During heavy rainfall the Spadefoot exhibits an explosive breeding response (Greenberg and Tanner 2004); these episodes are very obvious where they occur. Since the Avon Park area had a mean rainfall of 140 cm. during the first year of Franz survey (about 13 cm. higher than the long term mean; Geoff Shaughnessy, South Florida Water Management District, pers. comm.), spadefoot toads should have been very obvious at sandy sites if they genuinely occurred in the area. So much time was spent sampling the upland habitats during both the Banch-Hokit (2000) and Franz et al. (1998) surveys, even during rainy weather, and ponds were dip-netted for tadpoles during the Franz surveys, that it is unlikely that spadefoot toads were “missed”. Finally, based on museum records for Polk and Highlands Counties, two mammals (southeastern pocket gopher (Geomys pinetus) and wood rats (Neotoma floridana) should occur at APR, yet no burrow pushups of the gopher nor houses of the wood rats were observed, nor were any wood rats captured in the small mammal survey. Lead investigators in both surveys (Branch and Hokit 2000; Franz in Franz et. al. 1998) believed that dispersal of xeric-adapted fossorial species to the APR area may have been impeded by the unique geomorphologic isolation of the Bombing Range Ridge in combination with emerging habitats of the Lake Arbuckle drainage basin. Such a separation was confirmed for the scrub lizard by genetic studies (Clark et al. 1999).

The geographic range of some of the candidate species that “might” occur at APR stops in the central Florida counties just north of Avon Park (Table 8-3). APR is about 2/3 way down the Florida peninsula, and the ranges of many species from the Southeastern United States stop in Lake, Orange or Sumter Counties, about 1/3 way down the peninsula. Thus, APR is at the edge of the range for a number of species, so some of these species probably do not occur there. This decline in the number of vertebrate species as one progresses southward through Florida’s peninsula is termed the “peninsula effect”; Means and Simberloff (1987) proposed that this effect is due simply to reduction of habitats. This might be the case at APR with two salamanders, Plethodon grobmani and Desmognathus auriculatus, since the free flowing streams they require are a very minor habitat feature at the installation.

False Negatives and Detection Probability

Non-detection of a species at a site does not imply that the species is absent unless the probability of detection is 1 (MacKenzie et al. 2006). A major source of error found in the literature on estimation of biological diversity is detection error because few methods permit the detection of all species (Yoccoz et al. 2001). Thus, false negatives occur if a species was not detected at a site with the method used but actually occurred there. The jackknife equation indicated that between 9-19 species could have been missed. Many of the 36 species that could occur at APR (Table 8-3) could have been missed for reasons relating to detection probability. Franz et al. (1998) noted that 22 of the species that were only observed once or only a few times were “probably common” (in Franz et al. 1998), e.g., they were there, but had a low detection probability. This may hold true for some of the species that were not seen (Table 8-3). Many of the reasons I propose that these species were not

recorded, such as secretive behavior or very low population density, directly affect the probability that they will be seen, heard or captured. Probabilistic, repeated sampling at a number of sites is the recommended strategy (Nichols and Conroy 1996; Yoccoz et al. 2001) to account for detection probability.

The BH survey was an intensive survey directed at scrub habitat where patches were sampled repeatedly with a variety of methods over several years. Because of this repeated sampling, this survey probably detected both common and rare species, but in a relatively small section (scrub patches) of Avon Park. In contrast, the Franz survey was more extensive, occurring throughout the Range, thus the same sites or collection of species at a site was not always re-sampled. Common species were probably detected in almost all habitats, but some rare species throughout APR were probably missed.

Strictly speaking, detection probabilities computed from data analyzed with a capture-recapture model relate to the method or methods used to collect that dataset, so are method specific. Because many of the observations of species seen in the Franz et al. survey were made as chance observations (see quote at beginning of paper) incidental to the sampling methods and time periods employed for the focal species (Table 8-1), neither the methods used nor the sampling design was optimal for many of the counted species. Additionally, population densities of species with rapid turnover rates (anurans and lizards) may exhibit marked annual fluctuations (Enge 1997) and thus could be “missed”. Thus, we would expect that counts of some species would be “low” and counts of others species to be zero, when in fact the species occurs there.

Availability

Although tied together closely, the concepts of availability and detection are actually two distinct concepts. Availability relates the *possibility or impossibility* of detection, given that the species is there. Marsh and Sinclair (1989) separated bias due to lack of visibility into two components: 1) animals not being available (availability bias) and 2) animals not being detected even if they are available (perception bias). Availability bias is well recognized by biologists using distance sampling in marine mammal surveys; often the whales or dolphins being surveyed were there but underwater, and did not surface to be counted. This “habitat unavailability” is important if sampling occurs when a species has made a seasonal migration or is underground estivating. During prolonged drought conditions, Dodd (1993) found that striped newts (*Notophthalmus perstriatus*) would remain in refuges, waiting for better conditions, and thus be unavailable. Franz (1991) reported the barking tree frog (*Hyla gratoisa*) as a common resident at the Ordway Preserve in 1991, yet in two subsequent studies on the Preserve, neither Dodd (1992) nor Franz et al. (1995) heard or captured any, suggesting the species had vanished. Then, an adult was inadvertently dug from a *Geomys* mound during other research activities (Franz et al. 1995), indicating the barking treefrog had likely been there during the surveys, but was unavailable.

Detection relates to the *probability* of detecting a species, given that it is available for detection. This concept implies that the species is available in the habitat to be observed, heard, or detected by other means. The *probability* of being detected might be low, because the species may be secretive, or be very rare, but it is still available for detection if the right method and sampling intensity is used. Availability implies that the species is there; but it might be undetected if it is underground estivating during the survey. A population of

aestivating spadefoot toads can be very high, but because the probability of detection is essentially zero, the biologist might assume it is not present at the site.

For purposes of understanding why species are recorded or missed in these surveys, we can combine these two species attributes into four possibilities. Species that are both available and have a high detection probability are the ones that accumulate quickly on any list. Examples from this study were species that were very visible species (slow moving box turtles), species with colorful markings (corn snake), species that were so common they were likely to be encountered (armadillo), species that leave obvious structures or artifacts (Round-tailed muskrat, Gopher tortoise), or species with clear aural calls (green tree frog). Several species in this study fit the second category: they were available, but had a low detection probability due to rare status (Florida long-tailed weasel). A third category would be species that are not available during the survey, but have a high detection probability if available during the survey, e.g., the spadefoot toad. Finally, some species are not available during the survey and have a low detection probability if they would have been available during the survey, for example, fossorial species that exist at low densities. Only one specimen of the Florida worm lizard (Rhineura floridana) was found, and that was an incidental find while a researcher in the BH project was digging to place a drift fence.

However, this distinction between detection and availability is very artificial. I presented it for heuristic reasons because for many species we were not able to separate availability from detection probability in the Franz et al. (1998) survey because many sites were not re-visited repeatedly. This is an important concern because single visits to each site are commonly done in similar ecological surveys in the southeast. If sampling is done in a way that estimates detection probability (Nichols et al. 1998a), a statistically elegant

procedure has been devised to separate components of the population that are unavailable for detection from the component that is available for detection. Terrestrial salamander populations are largely subterranean, with only a few individuals near the surface available for capture on any given sampling occasion (Taub 1961). Bailey et al. (2004) estimated detection probability by sampling random plots repeatedly over three years using Pollock's Robust Design (Pollock 1982). She distinguished between a surface population (on the surface-available for capture) and a superpopulation (both in the ground-unavailable for capture, and on the surface-available for capture). Basing her work on Kendall and Nichols (1995), Kendall et al. (1997), and Kendall (1999), she was able to determine that 13% of the salamanders were available for capture during a given sampling period.

Sampling Bias of Methods Used

Biases of the sampling methods used probably contributed to the number of "missing species", as they would in any similar ecological inventory. The visual fox squirrel and gopher tortoise surveys conducted were biased due to variability that existed between observers or between different vegetation communities with differential "sightability" due to thickness of the vegetation. Coverboards can give biased detections due to the type of substrate used for the board or over-use (Marsh and Goicochea 2003). Some tadpole species may be more adept at avoiding dip nets than others, as with fish. In mammalian livetrapping studies, trap-shyness is a well recognized phenomenon, resulting in undetected individuals or species. Detection probability is directly related to trap effectiveness, which can vary depending on trap type (O'Farrell et al. 1994) or size (Maly and Cranford 1985). Anuran calling surveys were used extensively in the Franz survey, but night chorusing activity periods for some frog species can be so short that observers miss them entirely, or they may

be subdued, or the species may occupy a site but completely fail to chorus (Smith 2006). Detection probability for summer breeding can vary simply due to the protocol used and environmental covariates (Gooch et al. 2006). The loud airboats used to survey for round-tailed muskrat houses probably caused many herpetofaunal species to quickly retreat or hide, thus were undetectable.

Species Missed Because of Inappropriate or Insufficient Methods

King and Porter (2005) showed that a large sampling effort that included multiple sampling methods was the most effective manner of thoroughly sampling an ant assemblage in Florida, and this certainly holds true for vertebrates as well. In some of the APR surveys, some species were likely missed because the surveys did not use a method specifically tailored to detect them. Sherman traps were effectively used in the Franz survey to capture small mammals, but these are ineffective at capturing shrews. Short-tailed shrews in Florida utilize moist habitats (Brown 1997) and can be captured in pitfall traps, but the only pitfall traps used in these surveys were placed in the arid scrub plots. Larger live traps for mammals were not used during the Avon Park survey so the status of some of the intermediate sized vertebrate species was not determined. The slow moving striped skunk is commonly found as roadkill in areas of the United States where it is common; the extensive road-kill data in the Franz survey indicate that this is not a part of the fauna at Avon Park. Striped skunks are rare in some parts of Florida; Ehrhart (1976) did not catch this species in 77,068 nights of trapping at Canaveral National Seashore, using large Tomahawk traps and National Traps made for intermediate-sized mammals. The few spotted skunks captured in the Franz survey were captured in Sherman traps; they are likely more common than those trapping records indicate. My experience (Kinlaw et al. 1995) is that this species can be common in uplands

habitat but not observed; they prefer darker nights for activity periods. Nine of the 34 possible missing species were snakes, which were not sampled adequately because one of the best methods to catch snakes (trap arrays with funnel traps) were not used in either the BH (2000) or Franz et al. (1998) surveys.

A special problem is presented with species that have 3 dimensional activity or movement patterns. Only a few golden mice were captured with the 2-dimensional placement of Sherman traps on the surface of the ground; this species has a 3-dimensional arboreal home range, so traps placed along tree limbs would likely have increased detection probability. Pine snakes travel vertically down and laterally underground, utilizing burrows of pocket gophers or gopher tortoises (Franz 1992). Opportunities of observing them on the ground surface have a strong element of chance; only one record exists in these surveys. Because Mole kingsnakes spend most of the time underground, new innovative subterranean sampling methods would likely be required to detect it; such methods were not devised during these surveys. The southern Flying squirrel (*Glaucomys volans*) probably occurs at Avon Park but a specific trapping method and trap size appropriate for this species was not attempted, so it's occurrence was not recorded.

Because of limitations of each method, additional non-overlapping methods should be used, with each additional method having a different mode of detection, in order to reduce the bias associated with each method. Dividing up taxon into "detection guilds" as we do now with bird song or frog chorus surveys is needed, but many more methods are needed in faunal surveys than currently exist.

Species Characteristics, including Rareness

A species can be considered "rare" due to low abundance and/or small range size (Gaston 1994). Schoener (1987) characterized two types of rarity: 1) diffusive, referring to a species which is rare in certain parts of its range yet common in other parts; and 2) suffusive: a species that is rare everywhere. Two species that were commonly seen in these surveys, Sherman's fox squirrel and Florida mice, are rare in other parts of their range. Of the species not seen at APR (Table 8-3), the Florida panther, the mole kingsnake, and probably the short-tailed snake are clearly suffusive. Some species are suffusively rare because they may be on a trajectory towards extinction; e.g., pine snakes appear to be declining statewide, possibly due to habitat destruction (Ashton and Ashton 1981). Another species that was formerly abundant at many sites throughout Florida but has severely declined for unknown reasons is the common kingsnake (Lampropeltis getula, Krysko and Smith 2005). Two suffusive species that were seen (Rhineura floridana and Pituophis melanoleucus) on a single occasion at APR were also only observed at 2 scrub sites in a survey of 15 scrub patches by Mushinsky and McCoy (1995). Some species have been consistently reported as rare in certain areas for unknown reasons. Ophisarus attenuatus, the eastern slender glass lizard, was reportedly rare in south Florida in 1958 (Duelman and Schwartz 1958); this was still the case from 1988-98 at APR where only a single observation was made despite 10 years of surveys. Similarly, despite intensive sampling for vertebrates at the Ordway Preserve, Putnam County, FL, from 1983-1993, was conducted, five species had fewer than 5 sightings, including O. attenuatus (Franz 1995). Sometimes insufficient habitat is available. In Putnam County, woodrats were strongly associated with mesic hardwood hammock and bottomland hardwood swamp forests (HaySmith 1995). At APR no eastern woodrats were observed; only

1924 acres of hardwood swamp forest occurs there. A longer sampling time frame is clearly required to record the presence of rare species. Survey duration was more important than survey extent in California detection surveys for fishers and martens (Zielinski et al. 1997). Longer duration of sampling adds species: of the 5 rare species not observed by Branch and Hokit (2000), the Franz survey found 2 with additional sampling. An additional consideration is whether the sampling time frame is long enough to include periods of activity bursts or breeding eruptions of amphibians. For example, 85 Rana catesbeiana were captured on a single rainy night in one grid during the Branch survey.

When is a Species “Effectively Not There”?

When is a species “effectively not there”? This actually represents two questions. First, “What is the lowest probability at which a species is considered not there? This first question has been brought to the forefront of the scientific and popular press with recent articles by Fitzpatrick et al. (2005) and Hill et al. (2006) on credible evidence suggesting that the ivory billed woodpecker is still in existence, despite many, many routine bird surveys by amateur and professional ornithologists. Answering this question requires that the biologist confront the enigmatic issue of detection probability. The virtual explosion of papers dealing with this topic highlight the importance of avoiding the error of assuming that a species is not part of a community being sampled because they remain undetected due to cryptic behavior or very low population densities. The absence of evidence is not evidence of absence, as pointed out by the Scottish philosopher David Hume over 250 years ago.

What rarity could have been detected with the sample sizes used? This probability is $p = 1 - (1 - \alpha)^{1/N}$, where N is the number of sampling units, p is the probability of the species appearing in a single sampling unit, and α = the probability or confidence that the species

will be detected in the sample (McArdle 1990). For the Neoseps data, if we assume that the coverboard/raking procedure used in the BH survey is an optimal technique for detecting this species, with 5400 boards (Table 8-4), the magnitude of the sampling program used in the BH survey should have detected a rarity of about 1 out of 1000 Neoseps. Similarly, the 9440 livetraps used in the Franz et al. survey should have detected a woodrat a population as low as 1 out of 2000. Since neither species was detected, it is reasonable to assume safely that neither species was there. Moreover, both surveys used additional techniques to locate each species (searching for Neoseps tracks in the sand and Neotoma stick houses). While it is still possible they might occur at APR (remembering our woodpecker example and the quote at the beginning of this paper), it is very unlikely.

If these species could have been detected, what would have been the absolute maximum possible detection limit, given the sample sizes used? In medicine, this issue of zero numerators has been recognized since the 1970's. Physicians have been aware that zero side effects of a drug in n trials or zero morbidities from n surgeries did not necessarily mean no such events will occur in future trials, and created the "3 in n " rule of thumb (Rumke 1975, Hanley and Lippman-Hand 1983) as a bedside approximation to the maximum risk (the upper binomial confidence level). I computed exact 99% upper limits of detections for 4 of the undetected species and one of the detected species that had a very low density. The upper limits for these non-detected species are so low that the chances for detecting them using these field sampling methods are essentially negligible. Since the methods were optimal for capturing these species and the sample sizes were exceedingly large, the likelihood is that these 4 non-detected species did not occur at APR.

The second question is: should a species be considered as a biologically meaningful part of a community fauna if it is a “vagrant” species (Gaston 1994) which is not a permanent member of the assemblage, does not breed in the area, and has an extremely low density? For highly mobile species that visit an area on an irregular basis, the answer depends on the scale of the landscape being considered. During these surveys no sightings were made of Florida panther or black bear. These 2 mammals have a low density and move over very large home range sizes (95 km² for male and 20 km² for female black bears, McCown et al. 2004; 518 km² for males and 194 km² for female panther, Maehr et al. 1991). Certainly a large enough area (429 km²) exists at APR to maintain a few individuals of each species. While an occasional individual might traverse the area, it is not likely that either species are regular components of the faunal community at APR because they probably avoid the area due to the constant disturbance from military ground activities involving tanks and national guard troops combined with the intense noise levels from ground ordnance and aircraft overflights, which routinely break the sound barrier.

Conclusion

Anytime we use a model in ecology there are two possibilities: the data follow the model and the model can correctly predict future similar scenarios; or the data doesn't fit the model, so one can't use that model for prediction. In this study, these possibilities are: 1) additional species were there, but were “missed” in the field because they were not detected or were unavailable to be detected; or 2) the purported “missing” species were not there. A virtual explosion of papers has shown that failure to account for detection probability results in negatively biased estimates of species richness, e.g., some species are almost always “missed”; thus, my model is appropriate. In this study, the jackknife estimated a more

realistic estimate of the number of species, in spite of the comprehensive sampling efforts discussed.

Table 8-1. Sampling Methods and Intensities for 2 Surveys of Vertebrates at Avon Park Air Force Range, FL. during surveys by Branch and Hokit (2000) and Franz et al. (1998).

Target Species	Habitats Sampled	Sampling Method	Sampling Intensity
Branch/Hokit Survey	1994-98		
Scrub lizard	Scrub patches	Visual surveys x 4 yrs	67-95 patches
Gopher frogs, scrub lizards	Scrub patches	Trap arrays; drift fences with pitfall traps	3596 trapnights
Sand skinks and Blue-tailed mole skinks	Scrub patches	Coverboards and raking	> 4900 trapnights
Gopher frogs, scrub lizards	Scrub patches	Pitfall trapping grids	62,400 trapnights
Franz survey 1996-98			
Florida round-tailed muskrat	All wetland habitats	Systematic transects by foot and airboat	Partial and complete searches in 67 wetlands
Gopher tortoise	All upland habitats	Line transects, plot sampling for burrows	148 line transects totaling 101 km, 148 one hectare plots
Gopher frogs	Ponds, wetlands	Aural surveys, Dip nets and dredges	72 ponds visited for calls, 105 wetlands dip netted
Sherman's fox squirrel	Pine dominated upland habitats	Timed transects by foot	75 longleaf pine and 95 slash pine stands
Florida Mouse	Upland habitats	Sherman live traps	8160 trapnights on mobile and 1280 on permanent transects
Indigo snake and Eastern Diamondback rattlesnake	All habitats	"vigilant" observation during study	-----
All vertebrates	All roads used during study	Record road-kills and species observed	207 tours totaling 9333 miles

Table 8-2. List of vertebrates recorded at Avon Park Air Force Range, Florida (APR) during three separate surveys from 1988-1998.

REPTILES			
<u>Agkistrodon piscivorus</u> (Lacépède, 1789)	Cottonmouth	<u>Elaphe obsoleta</u> (Say 1823)	Yellow Rat Snake
<u>Alligator mississippiensis</u> (Daudin, 1803)	American Alligator	<u>Elaphe guttata</u> (Linnaeus, 1766)	Eastern Corn Snake
<u>Anolis carolinensis</u> (Voigt, 1832)	Green Anole	<u>Farancia abacura</u> (Holbrook, 1836)	Eastern Mud Snake
<u>Apalone ferox</u> (Schneider, 1783)	Florida Softshell	<u>Gopherus polyphemus</u> (Daudin, 1802)	Gopher Tortoise
<u>Cemophora coccinea</u> (Blumenbach, 1788)	Scarlet Snake	<u>Heterodon platirhinos</u> Latreille in Sonnini and Latrielle, 1801	Eastern Hognose Snake
<u>Chelydra serpentina</u> (Linnaeus, 1758)	Snapping Turtle	<u>Kinosternon baurii</u> (Garman, 1891)	Striped Mud Turtle
<u>Cnemidophorus sexlineatus</u> <u>sexlineatus</u> (Linnaeus, 1766)	Six-lined Racerunner	<u>Kinosternon subrubrum</u> <u>steindachneri</u> (Siebenrock, 1906)	Florida Mud Turtle
<u>Coluber constrictor</u> Linnaeus, 1788	Southern Black Racer	<u>Lampropeltis triangulum</u> (Lacépède, 1788)	Milksnake
<u>Crotalus adamanteus</u> Palisot de Beauvois, 1799	Eastern Diamondback	<u>Masticophis flagellum</u> <u>flagellum</u> (Shaw, 1802)	Eastern Coachwhip
<u>Deirochelys reticularia</u> (Latreille in Sonnini and Latrielle, 1801)	Chicken Turtle	<u>Micrurus fulvius</u> (Linnaeus, 1766)	Eastern Coral Snake
<u>Diadophis punctatus punctatus</u> (Linnaeus, 1766)	Southern Ringneck Snake	<u>N. fasciata pictiventris</u> (Cope 1895)	Florida Water Snake
<u>Drymarchon corais</u> (Boie, 1827)	Eastern Indigo Snake	<u>Nerodia floridana</u> (Goff, 1936)	Florida Green Water Snake
<u>Eumeces inexpectatus</u> Taylor, 1932	Southeastern Five-lined Skink	<u>O. compressus</u> (Cope, 1898)	Island Glass Lizard
<u>Opheodrys aestivus</u> (Linnaeus, 1766)	Rough Green Snake	AMPHIBIANS	
<u>Ophisarus attenuatus</u> Cope, 1880	Slender Glass Lizard	<u>Acris gryllus</u> (Le Conte, 1825)	Southern Cricket Frog
<u>Pseudemys nelsoni</u> Carr, 1938	Florida Redbelly Cooter	<u>Amphiuma means</u> Garden in Smith, 1821	Two-toed Amphiuma
<u>Pituophis melanoleucus mugitus</u> Barbour 1921	Eastern Pine Snake	<u>B. terrestris</u> (Bonnaterre, 1789)	Southern Toad
<u>Pseudemys peninsularis</u> Carr, 1938	Peninsula Cooter	<u>Bufo quercicus</u> Holbrook, 1840	Oak Toad
<u>Regina alleni</u> (Garman, 1874)	Striped Crayfish Snake	<u>Euryceaquadridigitata</u> (Holbrook, 1842)	Dwarf Salamander
<u>Rhadinaea flavilata</u> (Cope, 1871)	Pine Woods Snake	<u>Gastrophryne carolinensis</u> (Holbrook, 1836)	Eastern Narrowmouth toad
<u>Rhineura floridana</u> (Baird, 1858)	Florida Worm Lizard	<u>Hyla cinera</u> (Schneider, 1799)	Green Treefrog

Table 8-2 Continued.

AMPHIBIANS			
<u>Sceloporus woodi</u> Stejneger, 1918	Florida Scrub Lizard	<u>Hyla femoralis</u> Bosc in Daudin, 1800	Pine Woods Treefrog
<u>Scincella lateralis</u> (Say in James, 1823)	Ground Skink	<u>Hyla gratiosa</u> Le Conte, 1856	Barking Treefrog
<u>Seminatrix pygaea cyclas</u> Dowling, 1950	South Florida Swamp Snake	<u>Hyla squirella</u> Bosc in Daudin, 1800	Squirrel Treefrog
<u>Sistrurus miliaris barboura</u> Gloyd, 1935	Dusky Pigmy Rattlesnake	<u>Notophthalmus viridescens</u> <u>piaropicola</u> (Schwartz and Duellman, 1952)	Peninsula Newt
<u>Storeria dekayi victa</u> Hay, 1892	Florida Brown Snake	<u>Pseudacris nigrita</u> <u>verrucosa</u> (Cope, 1877)	Florida Chorus frog
<u>Tantilla relicta relicta</u> Telford 1966	Peninsula Crowned Snake	<u>Pseudacris ocularis</u> (Bosc and Daudin in Sonnini and Latreille, 1801)	Little Grass frog
<u>Terrapene anadens bauri</u> Taylor, 1894	Florida Box Turtle	<u>Pseudobranchus axanthus</u> <u>axanthus</u> Netting and Goin, 1942	Dwarf Siren
<u>Thamnophis sauritus</u> (Linnaeus, 1766)	Eastern Ribbon Snake	<u>Rana capito</u> Le Conte, 1855	Carolina Gopher Frog
<u>Thamnophis sirtalis sirtalis</u> (Linnaeus, 1758)	Eastern Garter Snake	<u>Rana catesbeiana</u> Shaw, 1802	Bullfrog
<u>Rana grylio</u> (Stejneger, 1901)	Pig Frog		
<u>Rana sphenoccephala</u> Cope, 1886	Southern Leopard Frog	MAMMALS	
<u>Siren anadensis</u> Linnaeus, 1766	Greater Siren	<u>Blarina carolinensis</u> Bachman 1837	Short-tailed Shrew
<u>Siren intermedia</u> Barnes, 1826	Lesser Siren	<u>Canis latrans</u> Say, 1823	Coyote
<u>Cryptotis parva</u> Say 1823	Least Shrew	<u>Procyon lotor</u> Linnaeus, 1758	Raccoon
<u>Dasyopus novemcinctus</u> Linnaeus, 1758	Nine Banded Armadillo	<u>Scalopus aquaticus</u> Linnaeus, 1758	Southern Mole
<u>Didelphis virginiana</u> Kerr 1792	Virginia Opossum	<u>Sciurus carolinensis</u> Gmelin, 1788	Gray Squirrel
<u>Lontra anadensis</u> Schreber, 1777	Neactic River Otter	<u>Sciurus niger</u> Linnaeus, 1758	Sherman's Fox Squirrel
<u>Lynx rufus</u> Schreber, 1777	Bobcat	<u>Sigmondon hispidus</u> Say and Ord, 1825	Hispid Cotton rat
<u>Mustela frenata</u> Lichtenstein, 1831	Long-tailed Weasel	<u>Spilogale putorius</u> Linnaeus, 1758	Spotted Skunk
<u>Neofiber alleni</u> True, 1884	Round-tailed Muskrat	<u>Sus scrofa</u> Linnaeus, 1758	Wild Boar
<u>Ochrotomys nuttalli</u> Harlan, 1832	Golden Mouse	<u>Sylvilagus floridanus</u> Allen, 1890	Eastern Cottontail
<u>Odocoileus virginianus</u> Zimmerman, 1780	White-tailed Deer	<u>Sylvilagus palustris</u> Bachman, 1837	Marsh Rabbit

Table 8-2 Continued.

MAMMALS			
<u>Oryzomys palustris</u> Harlan, 1837	Rice Rat	<u>Urocyon cinereoargenteus</u> Schreber, 1775	Gray Fox
<u>Peromyscus gossypinus</u> LeConte, 1853	Cotton Mouse	<u>Vulpes Vulpes</u> Linnaeus, 1758	Red Fox
<u>Peromyscus polionotus</u> Wagner, 1843	Oldfield Mouse		
<u>Podomys floridanus</u> (Chapman, 1889)	Florida Mouse		

Table 8-3. “Candidate” vertebrates that could potentially occur at Avon Park Range, FL, but were not recorded during three surveys from 1988-1998. Column 3 indicates if the geographic range of the species includes APR (APR), APR but Polk County only (APR-Polk), APR but Highlands County only (APR-Highlands), or if APR is at the edge (Edge) of the species’ range (with nearest counties) listed). Possible reasons why each species might have been missed in the surveys are listed.

Species	Common name	Geographic Range	Possible Explanation
<u>Ambystoma tigrinum</u> (Green, 1825)	Eastern Tiger salamander	Out (Hernando)	Insufficient sampling
<u>Clemmys guttata</u> (Schneider, 1792)	Spotted turtle	APR-Polk	Unsure
<u>Desmognathus auriculatus</u> (Holbrook, 1838)	Southern Dusky Salamander	APR-Polk	Probably extirpated, possibly declining statewide
<u>Eumeces egregius lividus</u> Mount, 1965	Bluetail Mole Skink	APR	“True Absence” see text
<u>Eumeces laticeps</u> (Schneider, 1801)	Broadheaded Skink	APR-Polk	Unsure
<u>Farancia erythrogramma</u> (Palisot De Beauvois in Sonnini and Latreille, 1801)	Rainbow Snake	Edge (Lake, Okeechobee)	Edge of range
<u>Puma concolor</u> Linnaeus, 1771	Eastern Cougar	APR	Extremely low density
<u>Geomys pinetis</u> Rafinesque, 1817	Pocket Gopher	APR	“True negative” see text
<u>Glaucomys volans</u> Linnaeus, 1758	Southern Flying Squirrel	APR	Did not sample for this species
<u>Heterodon simus</u> (Linnaeus, 1766)	Southern Hognose Snake	Edge (Lake)	Rare, sporadic distribution, declining statewide
<u>Hyla chrysoscelis</u> (Cope, 1880)	Cope’s Gray Tree Frog	Edge (Sumter)	Out of Range
<u>Lampropeltis getula getula</u> (Linnaeus, 1766)	Eastern Kingsnake	APR	Rare, declining statewide
<u>Lampropeltis calligaster rhombomaculata</u> (Holbrook, 1840)	Mole Kingsnake	Edge (Lake, Desoto)	Secretive, inappropriate sampling, low detection probability
<u>Mephitis Mephitis</u> Schreber, 1776	Striped Skunk	APR	Probably not there
<u>Neotoma floridana</u> Ord, 1818	Eastern Woodrat	APR	“True Absence” see text
<u>Neoseps reynoldsi</u> Stejneger, 1910	Florida Sand Skink	APR	“True Absence” see text
<u>Nerodia cyclopion</u> (Duméril, Bibron, and Duméril, 1854)	Green Water Snake	APR	Unsure
<u>Nerodia taxispilota</u> (Holbrook, 1838)	Brown Water Snake	APR	Unsure

Table 8-3 Continued.

Species	Common name	Geographic Range	Possible Explanation
<u>Notophthalmus perstriatus</u> (Bishop, 1941)	Striped Newt	Edge (Lake)	Edge of Range
<u>Ophisarus ventralis</u> (Linnaeus, 1766)	Eastern Glass Lizard	APR	Unsure, possibly not detected
<u>Plethodon grobmani</u> Allen and Neill, 1949	Slimy Salamander	APR-Polk	Inappropriate habitat; edge of range; Possibly not detected
<u>Pseudacris crucifer</u> (Wied-Neuwied, 1838)	Spring Peeper	Edge (Sumter, Osceola)	Edge of Range
<u>Pseudacris ornata</u> (Holbrook, 1836)	Ornate Chorus Frog	Edge (Lake, Hillsborough)	Edge of Range
<u>Pseudemys concinna</u> (LeConte, 1830)	Eastern River Cooter	Edge (Lake, Hillsborough)	Edge of Range
<u>Pseudotriton montanus</u> Baird, 1849	Eastern Mud Salamander	Edge (Lake, Orange)	Edge of Range
<u>Rana clamitans</u> Latreille in Sonnini and Latreille, 1801	Green Frog	Edge (Lake)	Edge of Range
<u>Rana heckscheri</u> Wright, 1924	River Frog	Edge (Lake, Hillsborough)	Edge of Range
<u>Regina rigida</u> (Say, 1825)	Glossy Crayfish Snake	Edge (Lake, Osceola)	Edge of Range
<u>Reithrodontomys humulis</u> Audubon and Bachman, 1841	Eastern Harvest Mouse	APR	Probably not there
<u>Scaphiopus holbrookii</u> (Harlan, 1835)	Spadefoot Toad	APR-Polk (Hardee)	“True Absence” see text
<u>Sceloporus undulates</u> (Latreille in Sonnini and Latreille, 1802)	Eastern Fence Lizard	APR-Polk	“True Absence” see text
<u>Sternotherus minor</u> (Agassiz, 1857)	Loggerhead Musk Turtle	APR-Highlands (and Lake)	Possibly not detected
<u>Stilosoma extenuatum</u> Brown, 1890	Short-tailed Snake	APR	Secretive, declining statewide
<u>Storeria occipitomaculata</u> (Storer, 1839)	Redbellied Snake	Sumter, Pasco	Out of Range
<u>Ursus americanus</u> Pallas, 1780	Black Bear	APR	Very low density
<u>Virginia valeriae</u> Baird and Girard, 1853	Smooth Earth Snake	APR-Highlands ¹	Rare, sporadic distribution

¹ Single questionable record.

Table 8-4. Sampling methods, effort, rarity that could have been detected, and binomial upper 95% confidence intervals for species detected zero or only a few times during two surveys conducted at Avon Park Air Force Range, FL, from 1994-98. N = number of detections; *p* = rarity that could have been detected with sample size and methods used, e.g., the probability of the species appearing in a single sampling unit (see text for details); Binomial C.I. = Upper 99% binomial confidence level for the entire sample, e.g., highest possible value that could be attained with the number of nondetections or detections, if the sampling trial follows the binomial distribution.

Species	Habitat Searched	Sampling Method	Sample Size	N	<i>p</i>	Binomial C.I. ³
<u>Neoseps reynoldsi</u>	Scrub ¹	Coverboard ¹	5,400	0	1 out of 1000	0.000980
<u>Eumeces egregius lividus</u>	Scrub ¹	Pitfall traps alone and with trap arrays ¹	Approx. 67,000	0	1 out of 10000	0.000079
<u>Sceloporus undulates</u> ⁴	Upland pine forests ² Scrub ¹	Pine stand searches for fox squirrel ² and scrub transect and quadrat surveys for tortoise burrows ²	177 pine stands 148 line transects and 148 quadrat surveys for burrows ²	0	1/4 out of 100	0.01114
<u>Neotoma floridana</u>	Upland habitats ²	Sherman live traps ²	9,440 trapnights	0	1 out of 2000	0.000561
<u>Ochrotomys nuttalli</u>	Upland habitats ²	Sherman live traps ²	9,440 trapnights	2	1 out of 2000	0.000982
<u>Nerodia cyclopion floridana</u>	All	Road-side observations and road-kills ²	207 tours	5	2 out of 100	0.06686

¹ Branch/Hokit survey from 1994-98

² Franz et al. survey from 1996-98

³ Computed with StatXact 3 for Windows, Cytel Software Corp.

⁴ Rarity statistics for fence lizard not directly comparable with other methods, because each transect or quadrat was considered a separate sampling occasion, but the fox squirrel and tortoise transects varied in distance and time.

CHAPTER 9 SUMMARY

The research presented in this dissertation was focused on the role of the burrow in arid or semi-arid regions. I present a considerable amount of new information on vertebrates and their burrows in upland habitats of Florida. My synthetic literature review (Chapter 2) illustrated not only that burrows are “hotspots” of biodiversity (Table 2-1) but have at least 9 key functions in the surrounding ecosystem. I suggested that burrows might develop emergent properties which could result in landscape level effects. There are many approaches a researcher can use to begin to understand the various roles of ground burrows. For example, how do they contribute to the organization and stability of the fauna in the surrounding area? I hope my conceptual model will only be a starting point for the direction of future studies.

The two primary excavators in the arid (scrub) and other upland communities of Florida are the gopher tortoise and the armadillo. Since the armadillo is a recent invader to Florida and is known to use the tortoise burrows, I was concerned that there could be negative impacts of this mammalian burrower on the chelonian. It would be challenging to design a research protocol that would result in a clear resolution to this issue. The observational surveys in Chapters 3 and 4 represent a beginning point in understanding how the burrows of each species are dispersed across the landscape. My finding that the dispersion parameter k did not vary among the habitats for each species indicated that both species dug their burrows in about the same spatial pattern. This finding was a little surprising. I also found that tortoises dig more in the scrub and armadillos more in the pine habitat. These results were supported by the literature and not surprising. Future research might be focused on

investigating whether armadillos move into areas already occupied by tortoises and usurp their burrows. Such research would clearly be long term.

What had previously been known about the architecture of these burrows was determined indirectly by techniques which were really not designed for that purpose. By blowing expanding foam down burrows at a relocation site near Clermont, FL, I was able to make foam casts of the three dimensional shapes of a few burrows and obtained some data on their geometry. There are obvious logistical limits to such a procedure, and the burrow has to be destroyed to retrieve the cast. By switching my methodology to ground penetrating radar, I obtained much better data on the underground geometry of these structures. By combining (for the first time) 2D GPR data with 3D visualization programs, I showed that the burrows had a “jagged corkscrew” shape (Chapter 5). Future investigations might focus on why this particular shape was so common among the images. For example, do tortoises have a handedness trait (e.g., right or left-handed)? The dramatic 3D GRP investigation (Chapter 6) was the first to fully expose the interrelatedness of these underground structures, showing the Florida mice burrows attached and circling the tortoise burrow spiral. The intriguing views of the large number of relict or “ghost” burrows exposed by the 3D radar illustrated that the underground zone in some scrub and sandhill regions of Florida might resemble a sponge or honeycomb, with numerous chambers that can serve as refugia for a variety of vertebrate and invertebrate species. We have reached a point with the GPR technology analogous to the point 20 years ago when 3D imaging was developed for the human body and presented to the medical community. The implications for understanding these underground communities are enormous.

If these burrows are “hotspots” of local biodiversity (Table 2-1) they may play a role in structuring the fauna in the local area surrounding each burrow. My estimate of 60-70 species using the tortoise burrows is conservative compared to earlier researchers. The burrow combination trap I developed is a new design that increases efficiency by capturing both the crawling/hopping trapping guild along with the flying guild. I had fewer anuran deaths using this design than with open bucket traps. Apparently humid air from the burrow prevented the captured individuals from becoming desiccated as rapidly as they would in the open bucket traps during the hot, dryer months. This is important because the primary anuran occupant of the burrows I sampled was the imperiled gopher frog, and a researcher needs a method to study them without unnecessary mortality. The standalone Malaise traps were also new designs that future researchers can use quickly to enlarge their sample size. My unique sampling protocol included multiple methods which allowed a thorough collection of the fauna using the burrows. The data collected following my method allowed the occupancy of many captured species to be estimated using the powerful new occupancy modeling procedure. In fact, the occupancy parameters presented in Chapter 7 for the gopher frog and Florida mice are the first to quantify this critical state variable for these threatened species.

The last chapter was not related to burrows but illustrate that burrow richness approached the vertebrate richness I found at Avon Park Air Force Range, a 43,000 hectare military installation. By using a model that allowed species not detected in 3 thorough surveys of the installation, I estimated the number of species missed. This provided the opportunity to consider the reasons why certain species are missed in such ecological surveys, information that is vital to organizations responsible for conducting them.

LIST OF REFERENCES

- Abaturov, B.D. 1972. The role of burrowing animals in the transport of mineral substances in the soil. *Pedobiologia* 12:261-266.
- Advani, R., and A.P. Jain. 1982. Burrowing patterns of sand-coloured rat, Rattus gleadowi. *Journal of the Bombay Natural History Society*, 79: 662-663.
- Allen, T., and T. Hoekstra. 1992. *Toward a unified ecology*. Columbia University Press, New York, NY 384 pp.
- Anderson, A.O., and D.M. Allred. 1964. Kangaroo rat burrows at the Nevada Test Site. *Great Basin Naturalist*, 24: 93.
- Anderson, D.R., K.P. Burnham, and G.C. White. 1994 AIC model selection in overdispersed capture-recapture data. *Ecology* 75:1780-1793.
- Andrusiak, L.A., and A.S. Harestad. 1989. Feeding behavior and distance from burrows of Columbian ground squirrels. *Canadian Journal of Zoology*, 67: 381-384.
- Apa, A.D., D.W. Uresk, and R.L. Linder. 1990. Black-tailed prairie dog populations one year after treatment with rodenticides. *Great Basin Naturalist*, 502: 107-113.
- Arnold, E.N. 1984. Ecology of lowland lizards in the eastern United Arab Emirates. *Journal of Zoology, London*. 204:329-354.
- ASDSO (Association of State Dam Safety Officials) 1999. Report on Specialty Workshop #1: Plant and animal impacts on earthen dams: One in a series of reports to FEMA on future research needs in dam safety. Association of State Dam Safety Officials, Inc. 450 Old Vine St, Lexington, KY.
- Ashton, R.E. Jr., and P. S. Ashton. 1988a. Handbook of reptiles and amphibians of Florida: Part one: the snakes. Windward Publishing, Inc. Miami, FL 176 pp.
- Ashton, R.E. Jr., and P. S. Ashton. 1991. Handbook of reptiles and amphibians of Florida: Part two: lizards, turtles and crocodilians. Windward Publishing, Inc. Miami, FL 191 pp.
- Ashton, R.E. Jr., and P. S. Ashton. 1988b. Handbook of reptiles and amphibians of Florida: Part three: the amphibians. Windward Publishing, Inc. Miami, FL 191 pp.
- Auffenberg, W., and R. Franz. 1982 The status and distribution of the gopher tortoise *Gopherus polyphemus*. In: Bury, R.B. (ed.). *North American Tortoises: Conservation and Ecology*. U.S. Fish and Wildlife Service, Wildlife Research Report 12, Washington, DC, pp 95-126.

- Auffenberg, W., and J.B Iverson. 1979. Demography of terrestrial turtles. Pp. 541-569 In: Harless, M. and Morlock, H. (eds.). *Turtles: Perspectives and research*. John Wiley and Sons, Inc., New York, NY, 712 pp.
- Aydelott, D.G., H.H. Bullock, A.L. Furman, H.O. White, and J.W. Spieth. 1968. Soil survey of Ocala National Forest Area, Florida. USDA Soil Conservation Service, Washington, D.C. 64 pages and maps.
- Bailey, H.H. 1924. The armadillo in Florida and how it reached there. *Journal of Mammalogy* 5:264-265.
- Bailey, L.L., T.R. Simons, and K.H. Pollock. 2004. Estimating detection probability parameters of *Plethodon* salamanders using the robust capture-recapture design. *Journal of Wildlife Management* 68:1-13.
- Bailey, W.J., and J.D. Roberts. 1981. The bioacoustics of the burrowing frog *Heleioporus* (Leptodactylidae). *15:693-702*.
- Bartholomew, G.A., and J.W. Hudson. 1961. Desert ground squirrels. *Scientific American*, 205: 107-116.
- Bauer, A., and A. Russell, 1991. Pedal specialisations in dune-dwelling geckos. *Journal of Arid Environments*, 20: 43-62.
- Behrends, P., M. Daly, and M. Wilson. 1985. Range use patterns and spatial relationships of Merriam's kangaroo rats *Dipodomys merriami*. *Behavior*, 96:187-209.
- Bell, S., E. McCoy, and H. Mushinsky. (eds.), 1991. *Habitat structure: the physical arrangement of objects in space*. Chapman and Hall, London. 464 pp.
- Bennet-Clark, H.C. 1987. The tuned singing burrow of mole crickets. *Journal of experimental biology*, 128:383-409.
- Blank, S., C. Seiter, and P. Bruce. 2001. *Resampling stats add-in for Excel user's guide*. Resampling Stats, Inc. Arlington, Virginia. 172 pp.
- Blankenship, E., and D. Thomas. 2005. Mechanical excavation of gopher tortoises for translocation using heavy equipment. *Herpetol. Rev.* 36:1: 38-41.
- Bliss, C.I. 1953. Fitting the negative binomial distribution to biological data. *Biometrics*. 9:176-196.
- Borchers, D.L., S.T. Buckland, and W. Zucchini. 2002 *Estimating animal abundance: closed populations*. Springer-Verlag, London. 332 pp.

Bowers, M.A., and J.H. Brown. 1992. Structure in a desert rodent community: use of space around *Dipodomys spectabilis* mounds. *Oecologia*, 92: 242-249.

Branch, L.C. 1993. Intergroup and intragroup spacing in the plains vizcacha, *Lagostomus maximus*. *Journal of Mammalogy*, 74 4: 890-900.

Branch, L.C., and D.G. Hokit. 2000. A comparison of scrub herpetofauna on two central Florida sand ridges. *Florida Scientist* 632:108-117.

Branch, L.C., D.Villarreal, and J.L.Hierro. 1999. Patterns of plant species diversity following local extinction of the plains vizcacha in semi-arid scrub. *Journal of Arid Environments* 41: 172-182.

Branch, L.C., D. Villarreal, J.L. Hierro, and K.M. Portier. 1996. Effects of local extinction of the plains vizcacha *Lagostomus maximus* on vegetation patterns in semi-arid scrub. *Oecologia*, 106: 389-399.

Breece, G.A., and J.L. Dusi. 1985. Food habits and home ranges of the common long-nosed armadillo *Dasypus novemcinctus* in Alabama. Pp. 419-427, In G.G. Montgomery (ed.) *The evolution and ecology of Armadillos, Sloths, and Vermilinguas*. Smithsonian Institution Press, Washington, DC. 451 pp.

Breining, D.R., P.A. Schmalzer, D.A. Rydene, and C.R. Hinkle. 1988 Burrow and habitat relationships of the gopher tortoise in coastal scrub and slash pine flatwoods on Merritt Island, Florida. Florida Game Fresh Water Fish Commission Nongame Wildlife Program. Final Report. Project GFC-84-016, Tallahassee. 313 pp.

Bronner, G.N. 1992. Burrow systems characteristics of seven small mammal species Mammalia: Insectivora; Rodentia; Carnivora. *Koedoe*, 351: 125-128.

Brose, U. 2002. Estimating species richness of pitfall catches by non-parametric estimators. *Pedobiologia* 46:101-107.

Brose, U., and N.D. Martinez. 2004. Estimating the richness of species with variable mobility. *Oikos* 1052: 292-300.

Brose, U., N.D. Martinez, and R.J. Williams. 2003. Estimating species richness: sensitivity to sample coverage and insensitivity to spatial patterns. *Ecology* 849:2365-2377.

Brown J.A., and M.D. Thomas. 2000 Residual trap-catch methodology for low-density possum populations. Report to Animal Health Board research contract R-80512. Research report UCDMS 2000/6, Biomathematics Research Centre, University of Canterbury, Christchurch, 29p.

- Brown, J.H., and E.J. Heske. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science*, 250: 1705-1707.
- Brown, L.N. 1997. A guide to the mammals of the southeastern United States. The University of Tennessee Press, Knoxville. 236 pp.
- Brown, R., E. Stone, and V. Carlisle. 1990. Soils. In: Myers, R. and Ewel, J. (eds.), *Ecosystems of Florida*, pp. 35-69. Orlando, FL: University of Central Florida Press. 765 pp.
- Buckland, S.T., D.R. Anderson, K.P. Burnham, and J.L. Laake. 1993 *Distance sampling: estimating abundance of biological populations*. Chapman and Hall, London. 446 pp.
- Buckland, S.T., D.R. Anderson, K.P. Burnham, and J.L. Laake, D.L. Borchers, and L. Thomas. 2001 *Introduction to distance sampling: estimating abundance of biological populations*. Oxford University Press. 448 pp.
- Buckland, S.T., D.R. Anderson, K.P. Burnham, and J.L. Laake, D.L. Borchers, and L. Thomas. 2004 *Advanced distance sampling*. Oxford University Press, 595 pp.
- Buffenstein, R. 1984. The importance of microhabitat in thermoregulation and thermal conductance in two Namib rodents—a crevice dweller, *Aethomys namaquensis*, and a burrow dweller, *Gerbillurus paeba*. *Journal of Thermal Biology*, 94: 234-241.
- Bulova, S.J. 1994. Patterns of burrow use by desert tortoises: influence of microclimate and chemical cues. PhD. Dissertation. University of Wisconsin. Madison, WI. 219 pp.
- Buol, S.W., F.D. Hole, R.J. McCracken, and R.J. Southard. 1997. *Soil Genesis and Classification*. 4th Ed. Iowa State University Press, Ames, IA. 527pp.
- Burke, R.L. 1989. Burrow-to-tortoise conversion factors: comparison of three gopher tortoise survey techniques. *Herpetological Review* 20:92-94.
- Burke, R.L., and J. Cox. 1988. Evaluation and review of field techniques used to study and manage gopher tortoises. Pp 205-215 In: *Management of amphibians, reptiles, and small mammals in North America*. Proceedings of the Symposium July 19021, Flagstaff, AZ. USDA Forest Service Gen. Techn. Rep. RM-166.
- Burnham, K.P. and D.R. Anderson. 2002. *Model selection and multimodal inference*. second edition, Springer-Verlag, New York 488 pp.
- Burnham, K.P., and W.S. Overton. 1978. Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika* 65:625-633.
- Burnham, K.P., and W.S. Overton. 1979. Robust estimation of population size when capture probabilities vary among animals. *Ecology* 60. pp. 927-936

- Burnham, K.P., D.R. Anderson, and J.L. Laake. 1980 Estimation of density from line transect sampling of biological populations. *Wildlife Monographs* No. 72, 1-202.
- Burns, J.A., D.L. Flath, and T.W. Clark. 1989. On the structure and function of white-tailed prairie dog burrows. *Great Basin Naturalist*, 49 4: 517-524.
- Butler, D. 1995. *Zoogeomorphology: animals as geomorphic agents*. Cambridge University Press, Cambridge, Massachusetts. 231 pp.
- Butler, J., T.J. Roper, and A.J. Clark. 1994. Investigation of badger Meles meles setts using soil resistivity measurements. *Journal of Zoology*, London 232:409-418.
- Butts, K.O., and J.C. Lewis. 1982. The importance of prairie dog towns to burrowing owls in Oklahoma. *Proceedings of the Oklahoma Academy of Science*, 62:46-52.
- Campbell, H.W., and S.P. Christman. 1982 The herpetological components of Florida sandhill and sand pine scrub associations. In: Scott, Jr. N.J., (ed.) *Herpetological Communities*. Wildlife Research Report 13, U.S. Fish and Wildlife Service, Washington.
- Campbell, T.M., and T.W. Clark. 1981. Colony characteristics and vertebrate associates of white-tailed and black-tailed prairie dogs in Wyoming. *American Midland Naturalist*. 105:269-276.
- Carlson, D.C., and E.M. White. 1988. Variations in surface-layer color, texture, pH, and phosphorous content across prairie dog mounds. *Soil Science Society of America Journal*, 52: 1758-61.
- Carpenter, C. 1982. The bullsnake as an excavator. *Journal of Herpetology*, 164: 394-401.
- Carthy, R.R., M.K. Oli, J.B. Wooding, J.E. Berish, and W.D. Meyer. 2005. Analysis of Gopher Tortoise population estimation techniques. US Army Corps of Engineers Construction Engineering Research laboratory, Champaign, Illinois, 35 pp.
- Caughley, G. 1977. *Analysis of Vertebrate Populations*. John Wiley and Sons, New York, NY. 234 pp.
- Ceballos, G., and J. Pacheco. 1999. Influence of prairie dogs (Cynomys ludovicianus) on habitat heterogeneity and mammalian diversity in Mexico. *Journal of Arid Environments*, 41(2): 161-172.
- Chew, R.M., and W.G. Whitford. 1992. A long-term positive effect of Kangaroo rats Dipodomys spectabilis on creosotebushes Larrea tridentata. *Journal of Arid Environments*, 22: 374-386.

Christman, S.P. 1988. Endemism in Florida's interior sand pine scrub. Final Project Report GFC-84-101. Florida Game and Fresh Water Fish Commission, Tallahassee.

Christman, S.P., and W.S. Judd. 1990. Notes of plants endemic to Florida scrub. Florida Scientist 53:52-73.

Clark, A.M., B.W. Bowen, and L.C. Branch. 1999. Effects of natural habitat fragmentation on an endemic lizard Sceloporus woodi: an historical perspective based on an mtDNA gene genealogy. Molecular Ecology 8:1093-1104.

Clark, W.K. 1951. Ecological life history of the armadillo in the eastern plateau region. American Midland Naturalist 46:337-358.

Clark, T. 1971. Notes on white-tailed prairie dog burrows. The Great Basin Naturalist, 313: 115-124.

Cochran, W.G. 1963. Sampling techniques, second edition. John Wiley and Sons, Inc., New York, NY. 405 pp.

Conant, R., and J.T. Collins. 1991. A field guide to reptiles and amphibians: Eastern and Central North America. Houghton Mifflin Company, Boston, 450 pp.

Conyers, Lawrence B. 2004. Ground-penetrating radar for archaeology. AltaMira Press, Walnut Creek, CA. 201 pp.

Cowan, C.D., W.R. Breakey, and P.J. Fischer. 1986. The methodology of counting the homeless. Proceedings of the Survey Research Methods Section, American Statistical Association, pp. 170-175.

Cox, J., D. Inkley D., and R. Kautz. 1987 Ecology and habitat protection needs of gopher tortoise Gopherus polyphemus populations found on lands slated for large-scale development in Florida. Florida Game and Fresh Water Fish Commission. Nongame Wildlife Program Technical Report No. 4. Tallahassee, FL. 75pp.

Daly, M., L. Jacobs, M. Wilson, and P. Behrends. 1992. Scatter hoarding by kangaroo rats Dipodomys merriami and pilferage from their caches. Behavioral Ecology, 3: 102-111.

Daniels, J.J., D. Harris., R. Roberts. And B. Schilling. 1992. GPR measurements for locating underground mine workings at an active open-pit mine. In: P. Hanninen and S. Autio (eds.), Fourth International Conference on Ground Penetrating Radar, Rovaniemi, Finland. pp. 237-245. Geologian tutkimuskeskus. Espoo, Finland

Davis, W.B., and D.J. Schmidly. 1994. The Mammals of Texas. Texas Parks and Wildlife, Austin, TX. 338 pp.

Dean, W.R.J., and S. Milton. 1991. Patch disturbances in arid grassy dunes: antelope, rodents, and annual plants. *Journal of Arid Environments*, 20: 231-237.

Diamond, J.M. 1975. Assembly of species communities. In: Cody, M.L. and Diamond, J.M. (eds.), *Ecology and Evolution of Communities*, pp. 342-444. Belknap Press of Harvard University, Cambridge, MA. 545pp.

Diemer, J.E. 1992. Gopher tortoise *Gopherus polyphemus* Daudin. In: P. Moler (ed.), *Rare and endangered biota of Florida Volume III. amphibians and reptiles*, pp.123-127. University Press of Florida, Gainesville, Florida. 291 pp.

Dodd, C.K. 1993. Cost of living in an unpredictable environment: the ecology of Striped Newts *Notophthalmus perstriatus* during a prolonged drought. *Copeia* 3:605-614.

Dodd, C.K. Jr. 1992. Biological diversity of a temporary pond herpetofauna in north Florida sandhills. *Biodiversity and Conservation*.1:125-142.

Douglass, J.F., and J.N. Layne. 1978 Activity and thermoregulation of the Gopher Tortoise *Gopherus polyphemus* in Southern Florida. *Herpetologica*. 34:359-374.

Duellman, W.E., and A. Schwartz. 1958. Amphibians and reptiles of southern Florida. *Bulletin of the Florida State Museum*. 35:181-324.

Efron, B., and R. Tibshirani. 1993 *An introduction to the bootstrap*. Chapman and Hall, New York. 425 pp.

Efron, B., and R. Tibshirani. 1986. Bootstrap measures for standard errors, confidence intervals, and other measures of statistical accuracy. *Statistical Science* 1:54-77.

Ehrhart, L.M. 1976. A study of a diverse coastal ecosystem on the Atlantic coast of Florida: mammal studies. Biomedical Office, National Aeronautics and Space Administration, J.F. Kennedy Space Center, Florida. 182 pp.

Eisenberg, J.F. 1983. The gopher tortoise as a keystone species. In: Bryant, R. and Franz, R. Eds, *The Gopher Tortoise: a keystone species*. Proceedings of the 4th Annual Meeting, pp.1-4. Gainesville, FL: Gopher Tortoise Council. Florida State Museum. 45 pp.

Elliott, J.M. 1971. Some methods for the statistical analysis of samples of benthic invertebrates. Scientific Publication No. 25. first edition. Freshwater Biological Association, The Ferry House, Ambleside, UK, 148 pp.

Ellison, G.T.H. 1993. Group size, burrow structure and hoarding activity of pouched mice *Saccostomus campestris*: Cricetidae in southern Africa. *African Journal of Ecology*, 31: 135-155.

Enge, K.M. 1997. Habitat occurrence of Florida's native amphibians and reptiles. Technical Report No. 16. Florida Game and Fresh Water Fish Commission, Tallahassee, FL, 44 pp.

Epperson, D.M. 1997. Gopher tortoise (Gopherus polyphemus) populations: activity patterns, Upper respiratory Tract Disease, and management on a military installation in Northeast Florida. M.S. Thesis, University of Florida, Gainesville.

Ernst, C., and R. Barbour. 1972. Turtles of the United States. University Press of Kentucky, Lexington, KY. 341 pp.

Estes, T.O., and T.M. Mann. 1996. State land 16th section gopher tortoise survey. Mississippi Technical Report No. 43, Mississippi Department of Wildlife, Fisheries, and Parks. 37pp.

Evans, F.C. 1951. Notes on a population of the striped ground squirrel Citellus tridecemlineatus in an abandoned field in southeastern Michigan. Journal of Mammalogy, 32: 437-449.

Feldhamer, G. 1979. Vegetative and edaphic factors affecting abundance and distribution of small mammals in southeast Oregon. The Great Basin Naturalist 39:207-218.

Fitch, H.S. 1948. Ecology of the California ground squirrel on grazing lands. American Midland Naturalist, 39: 513-596.

Fitch, H.S., P. Goodrum, and C. Newman. 1952. The armadillo in the Southeastern United States. Journal of Mammalogy 33:121-37.

Fitzpatrick J. W., M. Lammertink, M. D. Luneau, Jr., T. W. Gallagher, B. R. Harrison, G. M. Sparling, K. V. Rosenberg, R. W. Rohrbaugh, E. C. H. Swarthout, P. H. Wrege, S.B. Swarthout, M. S. Dantzker, R. A. Charif, T. R. Barksdale, J. V. Remsen, Jr., S. D. Simon, and D. Zollner. 2005. Ivory-billed Woodpecker Campephilus principalis persists in continental North America. Science 308:1460-1462.

Florida Fish and Wildlife Conservation Commission 2006a Florida Fish and Wildlife Conservation Commission Meeting Agenda, June 708, 2006, West Palm Beach, FL Consideration of Phase 1 of the Listing Process for the Gopher Tortoise. <http://myfwc.com/commission/2006/June/index.html>. 2006a Accessed June 24, 2006.

Florida Fish and Wildlife Conservation Commission 2006b Notice of proposed rulemaking. Rule No: 68A-27.005. Proposed Rule to define a gopher tortoise burrow. <http://myfwc.com/commission/2006/June/index.html>. 2006 Accessed June 24, 2006.

Florida Natural Areas Inventory 2004 1018 Thomasville Road, Suite 200-C, Tallahassee, Florida 32303. <http://www.fnai.org/descriptions.cfm>, Accessed November 4, 2004.

Flosser, R. 1984. Five colonies of the hairy-nosed wombat, Lasiorhinus latifrons Owen, 1845 in the Brookfield Conservation Park in South Australia. *Zoologischer Anzeiger Jena*, 213: 224-233.

Ford, R.D., J. M. Robbins, Jr., J.T. Werner, D. Cowherd, C.N. Gordon, W.B. Warmack, M.M. Brown, K.W. Monroe, W.G. George, T. Sanders, and P.M. Basch. 1990. Soil survey of Polk County, Florida. USDA Soil Conservation Service, Washington, D.C. 235 pages and maps.

Frank, C.L. 1988a. Diet selection by a heteromyid rodent: role of net metabolic water production. *Ecology*, 69: 1943-1951.

Frank, C.L. 1988b. The influence of moisture content on seed selection by kangaroo rats. *Journal of Mammalogy*, 69: 353-357.

Frank, C.L. 1988c. The relationship of water content, seed selection, and the water requirements of a heteromyid rodent. *Physiological Zoology*, 61: 527-534.

Franz, R. 1986. Gopherus polyphemus gopher tortoise Burrow commensals. *Herpetol. Rev.* 17:64.

Franz, R. 1991. Annotated list of the vertebrates of the Katharine Ordway Preserve-Swisher Memorial Sanctuary, Putnam County, Florida 1983-1989. Ordway Preserve Research Series, Report No 2, 41 pp.

Franz, 1992. Florida Pine Snake. Pp. 254-258 In: P. E. Moler, (ed.) Rare and Endangered Biota of Florida Volume III. Amphibians and Reptiles. University Press of Florida, Gainesville. 291 pp.

Franz, R. 1995. An introduction to the amphibians and reptiles of the Katharine Ordway Preserve-Swisher Memorial Sanctuary, Putnam County, Florida. *Bulletin of the Florida Museum of Natural History*. 381:1-10.

Franz, R., D. Maehr, A. Kinlaw, C. O'Brien, and R. Owen. 1998. Avon Park Air Force Range Project: Distribution and Abundance of Sensitive Wildlife Species at Avon Park Air Force Range. Final Report, Project RWO-169, Natural Resources Flight, Avon Park Air Force Range, Florida.

Franz, R., R.E. Ashton, and W.W. Timmerman. 1995. Behavior and movements of certain small sandhill amphibians and reptiles in response to drift fences. Nongame Wildlife Program project GFC-87-023. Florida Game and Fresh Water Fish Commission, Tallahassee.

Frase, B.A. and K.B. Armitage. 1984. Foraging patterns of yellow-bellied marmots: role of kinship and individual variability. *Behavioral Ecology and Sociobiology*, 16: 1-10

Friend, G.R. 1993. Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia: a review. *Biological Conservation*, 65: 99-114.

Fullagar, P.K. and D. Livleybrooks. 1994. Trial of tunnel radar for cavity and ore detection in the Sudbury Mining Camp, Ontario. In: D. Redman Chair, Proceedings of the Fifth International Conference on Ground Penetrating Radar: 883-894. Waterloo Centre for Groundwater Research, Waterloo, Canada.

Futuyma, D.J. 1994. The evolution and importance of species interactions. In: Meffe, G. and Carroll, C. (eds.), *Principles of conservation biology*, pp. 213-218. Sunderland: Sinauer Associates, Inc. 600 pp.

Fylstra, D., L. Lasdon, J. Watson, and A. Warren. 1998. Design and use of the Microsoft Excel Solver. *Interfaces*, September-October. 28: 5: 29-55.

Gahr, M. 1992. Distribution of Pygmy rabbit Brachylasus idahoensis: burrows in sagebrush flats, Washington. *Northwest Science*, 66 2: 125.

Galbreath, G.J. 1980. Aspects of natural selection in Dasypus novemcinctus. Ph.D. Dissertation, University of Chicago, Chicago, IL 102 pp.

Galbreath, G.J. 1982. Armadillo, Dasypus novemcinctus. Pp. 71-79 In: J.A. Chapman, and G.A. Feldhamer (eds.) *Wild Mammals of North America*. The Johns Hopkins University Press, Baltimore, MD. 1147 pp.

Gardner, J.A., and J.L. Landers. 1981. Food and habitat of the gopher tortoise in southwestern Georgia. *Proc. 35th Ann. Conf. Southeastern Assoc. Game Fish Comm.* Pp. 120-134.

Gaston, K.J. 1994. *Rarity*. Chapman and Hall, London. 205pp.

Gause, G.E. 1980. Physiological and morphometric responses of the Nine-Banded Armadillo Dasypus novemcinctus to Environmental Factors. Ph.D. Dissertation, University of Florida, Gainesville, FL. 112 pp.

Gibson, D.J. 1989. Effects of animal disturbance on tallgrass prairie vegetation. *American Midland Naturalist*, 121: 144-154.

Godley, J.S. 1992. Gopher Frog Rana capito Le Conte In: Moler, P. (ed.) *Rare and Endangered Biota of Florida Volume III. Amphibians and Reptiles*. University Press of Florida, Gainesville. 291 pp.

Goin, C.J., O.B. Goin, and G.R. Zug. 1962. *Introduction to herpetology* third edition. W.H. Freeman and Company, New York, NY. 378 pp.

Gooch, M.M., A.H. Heupel, S.J. Price, and M.E. Dorcas. 2006. The effects of survey protocol on detection probabilities and site occupancy estimates of summer breeding anurans. *Applied Herpetology* 32:129-142.

Gordon, G., T. Riney, J. Toop, B.C. Lawrie, and M.D. Godwin. 1985. Observations on the Queensland Hairy-nosed Wombat, Lasiorhinus krefftii Owen. *Biological Conservation*, 33:165-195.

Grasmueck, M., R. Weger, and H. Horstmeyer. 2005. Full-resolution 3D GPR imaging. *Geophysics* 70(1):K12-K19.

Gray, H.L., and W.R. Schucany. 1972. *The generalized jackknife statistic*. Marcel Dekker, Inc, New York, New York, USA, 308 pp.

Green, R.H. 1979. *Sampling design and statistical methods for environmental biologists*. John Wiley and Sons, New York. 257pp.

Green, R.H. 1966. Measurement of non-randomness in spatial distributions. *Research in Population Ecology* 8:1-7.

Greenberg, C.H., and G.W. Tanner. 2004. Breeding pond selection and movement patterns by Eastern Spadefoot toads Scaphiopus holbrookii in relation to weather and edaphic conditions. *Journal of Herpetology* 38:569-577.

Greer, A.E. 1989. *Biology and evolution of Australian lizards*. Chipping Norton, NSW: Surrey Beatty and Sons PTY Limited. 264 pp.

Guo, Q. 1996. Effects of bannertail kangaroo rat mounds on small-scale plant community structure. *Oecologia*, 106: 247-256.

Guyer, C., and S.M. Hermann. 1997. Patterns of size and longevity of gopher tortoise Gopherus polyphemus burrows: implications for the longleaf pine ecosystem. *Chelonian Conservation and Biology*. 2:507-513.

Halliday, T., and K. Adler. 1986. *The encyclopedia of reptiles and amphibians*. Facts on File, New York, NY. 160 pp.

Hanley, J.A., and A. Lippman-Hand. 1983. If nothing goes wrong, is everything all right? Interpreting zero numerators. *JAMA* 249 13 17431745.

Hansell, M.H. 1993. The ecological impact of animal nests and burrows. *Functional Ecology*, 7: 5-12.

Hatough-Bouran, A. 1990. The burrowing habits of desertic rodents *Jaculus jaculus* and *Gerbillus dasyurus* in the Shaumari Reserve in Jordan. *Mammalia*, 54 3: 341-359 .

Haug, E.A., B.A. Millsap, and M.S. Martell. 1993. Burrowing Owl. The Birds of North America, No. 61. Philadelphia, PA: The Academy of Natural Sciences of Philadelphia. 19 pp.

Hawkins, L.K., and P.F. Nicoletto. 1992. Kangaroo rat burrows structure the spatial organization of ground-dwelling animals in a semi-arid grassland. *Journal of Arid Environments*, 23: 199-208.

HaySmith, L. 1995. Neotoma floridana floridana: Natural history, populations, and movements in north-central Florida. *Bulletin of the Florida Museum of Natural History* 38 Pt. II:211-243.

Heinz, J., and T. Aigner. 2003. Three-dimensional GPR analysis of various Quaternary gravel-bed braided river deposits southwestern Germany. In: C.S. Bristow and H.M. Jol (eds.), *Ground Penetrating Radar in Sediments*. Pp. 99-110. Geological Society Special Publication No. 211, The Geological Society, London.

Hellman, J.J., and G.W. Fowler. 1999. Bias, precision, and accuracy of four measures of species richness. *Ecological Applications* 9:824-834.

Heltsh, J.F., and N.E. Forrester. 1983. Estimating species richness using the jackknife procedure. *Biometrics* 39:1-11.

Hill, G. E., D. J. Mennill, B. W. Rolek, T. L. Hicks, and K. A. Swiston. 2006. Evidence suggesting that Ivory-billed Woodpeckers Campephilus principalis exist in Florida. *Avian Conservation and Ecology - Écologie et conservation des oiseaux* 13: 2. [online] URL: <http://www.ace-eco.org/vol11/iss3/art2/>. Accessed October 15, 2006.

Hines, J.E., Boulinier, T., Nichols, J.D., Sauer, J.R., and Pollock, K.H. 1999. COMDYN: Software to study the dynamics of animal communities using a capture-recapture approach. *Bird Study* 46 Suppl., S209-S217.

Hipes, D., D.R. Jackson, K. NeSmith, D. Printiss, and K. Brandt. 2001. Field guide to the rare animals of Florida. Florida Natural Areas Inventory, Tallahassee, unnumbered.

Hole, F.D. 1981. Effects of animals on soil *Geoderma*, 25: 75-112.

Holmes, W.G. 1984. Predation risk and foraging behavior of the hoary marmot in Alaska. *Behavioral Ecology and Sociobiology*, 15: 293-301.

Humphrey, R.R. 1974. Zoogeography of the nine-banded armadillo in the United States. *Bioscience* 24:457-462.

Humphrey, S.R. 1992. . Rare and endangered biota of Florida. Volume I. Mammals. University Press of Florida, Gainesville, FL 392 pp.

Inbar, M., and R.T. Mayer. 1999. Spatio-temporal trends in armadillo diurnal activity and road-kills in central Florida. *Wildlife Society Bulletin*. 273:865-872.

IUCN. 1996. 1996 IUCN red list of threatened animals. ICUN, Gland, Switzerland.

Jackson, D.R., and Milstrey, E.G., 1989. The fauna of gopher tortoise burrows. In: Diemer, J.E., D.R. Jackson, J.L. Landers, J.N. Layne, and D.A. Wood. (eds.). Gopher tortoise relocation symposium proceedings, pp. 86-98. Tech. Rep. No. 5. Tallahassee, FL: Florida Games and Fresh Water Fish Commission, Nongame Wildlife Program Technical Report #5. 109 pp.

Jacob, A.P. 1940. The fauna of soil. *Quarterly review of biology*, 15: 28-58.

Jones, C.A., and R. Franz. 1990. Use of gopher tortoise burrows by Florida mice Peromyscus floridanus in Putnam County, Florida. *Florida Field Nat.* 18:45-68.

Jones, C.G., J.H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos*, 69: 373-386.

Jones, W.T. 1984. Natal philopatry in bannertailed kangaroo rats. *Behavioral Ecology and Sociobiology*, 15: 151-155.

Kaczor, S.A., and D.C. Hartnett. 1990. Gopher tortoise Gopherus polyphenus: effects on soils and vegetation in a Florida sandhill community. *American Midland Naturalist* 123: 100-111

Kalisz, P.J., and W.H. Davis. 1992. Effect of prairie voles on vegetation and soils in central Kentucky. *American Midland Naturalist*, 127: 392-399.

Kay, F.R., and W.G. Whitford. 1978. The burrow environment of the banner-tailed kangaroo rat, Dipodomys spectabilis, in south-central New Mexico. *American Midland Naturalist*, 99: 270-279.

Kays, R.W., and D.E. Wilson. 2002. *Mammals of North America*. Princeton University Press, Princeton, NJ. 240 pp.

Kendall, W.L. 1999. Robustness of closed capture-recapture methods to violations of the closure assumption. *Ecology* 80:2517-2525.

Kendall, W.L., and J.D. Nichols. 1995. On the use of secondary capture-recapture samples to estimate temporary emigration and breeding proportions. *Journal of Applied Statistics* 22:751-762.

Kendall, W.L., J.D. Nichols, and J.E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78:563-578.

- Killion, M.J., W.E. Grant, and S.B. Vinson. 1995. Response of Baiomys taylori to changes in density of imported fire ants. *Journal of Mammalogy*, 761: 141-147.
- King, D. 1980. The thermal biology of free-living sand goannas Varanus gouldii in southern Australia. *Copeia*, 4: 755-767.
- King, J.A. 1959. The social behavior of prairie dogs. *Scientific American* 201:128-140.
- King, J.R., and S.D. Porter. 2006. Evaluation of sampling methods and species richness estimators for ants in upland ecosystems in Florida. *Environmental Entomology* 346:1566-1578.
- Kingdon, J. 1990. *Arabian mammals: a natural history*. London: Academic Press. 279 pp.
- Kinlaw, A.E. 1990. Estimation of a spotted skunk Spilogale putorius population with the Jolly-Seber model and an examination of violations of model assumptions. M.S. Thesis, North Carolina State University, Raleigh, NC. 202 pp.
- Kinlaw, A.E. 1999. A review of burrowing by semi-fossorial vertebrates in arid environments. *J. Arid Environ.* 41:127-145.
- Kinlaw, A.E., L. M. Ehrhart, and P.D. Doerr. 1995. Spotted skunks Spilogale putorius ambarbalis trapped at Canaveral National Seashore and Merritt Island, Florida. *Florida Field Naturalist* 233: 57-86.
- Knizley, E.J. 1997. Gopher tortoise (Gopherus polyphemus) relocation project: monitoring the tortoise population and associate species of the tortoise burrow. M.S. Thesis. University of Florida, Gainesville.
- Koford, C.B. 1958. Prairie dogs, whitefaces, and blue grama. *Wildlife Monographs* 3:1-78.
- Kolb, H.H. 1991. Use of burrows and movements by wild rabbits Oryctolagus cuniculus on an area of sand dunes. *Journal of Applied Ecology*, 28: 879-891.
- Kolb, H.H. 1994. The use of cover and burrows by a population of rabbits *Mammalia*: Oryctolagus cuniculus in eastern Scotland. *Journal of Zoology*, London. 233: 9-17.
- Kowalski, K and B. Rzebik-Kowalska. 1991. *Mammals of Algeria*. Polish Academy of Sciences, Wroclaw, Poland. 370 pp.
- Krebs, C.J. 1999. *Ecological Methodology*. second edition. Addison Wesley Longman Inc., Menlo Park, CA. 620 pp.

Krysko, K.L., and D.J. Smith. 2005. The Decline and Extirpation of the kingsnake in Florida, pp.132-141 In: W.E. Meshaka, Jr. and K.J. Babbitt, eds Amphibians and Reptiles: Status and Conservation in Florida. Krieger Publish Company, Melbourne, FL 334 pp.

Lange, J.H., R.E. LaPorte, E.O. Talbott, Y.F. Chang. 2003. Capture-recapture method: the gold standard for incidence and prevalence Letter. New Zealand Medical Journal 1176:116.

Laundre, J.W., and T.D. Reynolds. 1993. Effects of soil structure on burrow characteristics of five small mammal species. Great Basin Naturalist, 534: 358-366.

Laundre, J.W. 1989. Horizontal and vertical diameter of burrows of five small mammal species in southeastern Idaho. Great Basin Naturalist, 49: 646-649.

Laundre, J.W. 1993. Effects of small mammal burrows on water infiltration in a cool desert environment. Oecologia, 94: 43-48.

Layne, J.N., and R. J. Jackson. 1994. Burrow use by the Florida mouse Podomys floridanus in south-central Florida. American Midland Naturalist, 131: 17-23.

Layne, J.N. 1992. Florida Mouse Podomys floridanus In: Humphrey, S.R.. (ed.) Rare and Endangered Biota of Florida Volume I. Mammals. University Press of Florida, Gainesville. 392 pp.

Layne, J.N., and A.M. Waggener, Jr. 1984. Above-ground nests of the nine-banded armadillo in Florida. Florida Field Naturalist 12:58-61.

Layne, J.N., and D. Glover. 1977. Home range of the armadillo in Florida. Journal of Mammalogy 583:411-413.

Levine, R.H., R.R. Parmenter, and J.W. Brunt. 1995. Wildfire in desert grassland: effects on the burrow occupancy and home range of the banner-tailed kangaroo rat Dipodomys spectabilis in central New Mexico. Bulletin of the Ecological Society of America, 76 Suppl. 3: 356.

Loffler, E., and C. Margules. 1980. Wombats detected from space. Remote Sensing of Environment, 9: 47-56.

Louw, G.N. and M.K. Seely. 1982. Ecology of Desert Organism. London and New York:Longman. 194pp.

Luckenbach, R.A. 1982. Ecology and Management of the Desert Tortoise Gopherus agassizii in California. In: Bury, R.B. (ed.), North American Tortoises: Conservation and ecology, pp.1-37. Washington, D.C.: United States Department of the Interior, Fish and Wildlife Service Wildlife Report 12, 126 pp.

Lynch, C.D. 1980. Ecology of the suricate, Suricata suricatta and yellow mongoose, Cynictis penicillata with special reference to their reproduction. Memoirs van die Nasionale Museum, No. 14. National Museum, Bloemfontein, South Africa. 145 pp.

Lynch, C.D. 1983. The mammals of the Orange Free State. Memoirs van die Nasionale Museum, No. 18. National Museum, Bloemfontein, South Africa. 218 pp.

MacKenzie, D.I., J.D. Nichols, N. Sutton, K. Kawanishi, and L.L. Bailey. 2005. Improving inferences in population studies of rare species that are detected imperfectly. *Ecology* 86:1101-1113.

MacKenzie, D.I., J.D. Nichols, J.A. Royle, K.H. Pollock, L.L. Bailey, and J.E. Hines. 2006. *Occupancy estimation and modeling: Inferring Patterns and dynamics of species occurrence*. Academic Press, Burlington, MA. 324 pp.

Maehr, D.S., E.D. Land, and J.C. Roof. 1991. Social ecology of Florida Panthers. *National Geographic Research and Exploration*. 74: 414-431.

Malhado, A.C.M., and M. Petrere, Jr. 2004. Behaviour of dispersion indices in pattern detection of a population of angico, *Anadenanthera peregrina* Leguminosae. *Brazilian Journal of Biology* 64: 243-249.

Mallory, F.F., and T.D. Heffernan. 1987. Floristic modification of low arctic tundra by the Arctic ground squirrel, Spermophilus parryii. *Canadian Field-Naturalist*, 101:388-391.

Maly, M.S., and J.A. Cranford. 1985. Relative capture efficiency of large and small Sherman live traps. *Acta Theriologica* 30:165-167.

Manly, B.F.J. 1997 *Randomization, bootstrap and Monte Carlo methods in biology*. Chapman and Hall, New York. 342 pp.

Mares, M.A., R.A. Ojeda, and R.M. Barquez. 1989. *Guide to the mammals of Salta Province, Argentina*. University of Oklahoma Press, Norman, OK. 303 pp.

Marsh, D.M., and M.A. Goicochea. 2003. Monitoring terrestrial salamanders: biases caused by intense sampling and choice of cover objects. *Journal of Herpetology* 37:460-466.

Marsh, H., and D.F. Sinclair. 1989. Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. *Journal of Wildlife Management* 53:1017-1024.

McArdle, B.H. 1990. When are rare species not there? *Oikos* 57:276-277.

McCown, W., P. Kubilis, T. Eason, and B. Scheick. 2004. Black Bear movements and habitat use relative to roads in Ocala National Forest. Final Report Contract BD-016, Florida Department of Transportation and Florida Fish and Wildlife Commission, Tallahassee.

- McCoy, E.D., and H.R. Mushinsky. 1995 The demography of Gopherus polyphemus Daudin in relation to size of available habitat. Final Project Report. GFC-86-013. Nongame Wildlife Program. Florida Game and Fresh Water Fish Commission, Tallahassee.
- McCoy, E.D., and H.R. Mushinsky. 1992 Studying a species in decline: Gopher Tortoises and the dilemma of correction factors. *Herpetologica* 48: 402-407.
- McDonough, C.M., and W.J.Loughry. 2001. Armadillos. Pp.796-799, In: D. MacDonald, and S. Norris (eds.). *The Encyclopedia of Mammals*. Vol. III. Marsupials, insect eaters, and small herbivores. Facts on File, Inc., New York, NY. 930 pp.
- McDonough, C.M., M.A. DeLaney, P.Q. Le, M.S. Blackmore, and W.J. Loughry. 2000. Burrow characteristics and habitat associations of armadillos in Brazil and the United States of America. *Revista de Biologia Tropical* 48: 109-120.
- McLachlan, J.S., and J.S. Clark. 2004. Reconstructing historical ranges with fossil data at continental scales. *Forest Ecology and Management* 197: 139-147.
- McLean, I.G. 1978. Plugging of nest burrows by female Spermophilus columbianus. *Journal of Mammalogy*, 59: 437-439.
- McNab, B.K. 1980. Energetics and the limits to a temperature distribution in armadillo. *Journal of Mammalogy* 61:606-627.
- McRae, W.A., Landers, J.L., and Garner, J.A. 1981. Movement patterns and home range of the Gopher Tortoise. *American Midland Naturalist*, 106:165-179.
- Meadows, P.S. 1991. The environmental impact of burrows and burrowing animals- conclusions and a model. In: P.S. Meadows and A. Meadows (eds.), *The environmental impact of burrowing animals and animal burrows: proceedings of a symposium held at the Zoological Society of London* pp. 327-338. The Zoological Society of London, London, United Kingdom, 319 pp.
- Meadows, P.S., and A. Meadows. 1991. The environmental impact of burrowing animals and animal burrows. proceedings of a symposium held at the Zoological Society of London, May, 1990. Zoological Society of London. 319 pp.
- Means, D.B., and D. Simberloff. 1987. The peninsula effect: habitat-correlated species decline in Florida's herpetofauna. *Journal of Biogeography* 14:551-568.
- Meyers, J.M., and D.A. Pike. 2006. Herpetofaunal diversity of Alligator River National Wildlife Refuge, North Carolina. *Southeastern Naturalist* 52:235-252.

Mills, L.S., Soule, M.E., and Doak, D.F. 1993. The keystone species concept in ecology and conservation. *Bioscience*, 43: 219-224.

Milstrey, E.G., 1987. Bionomics and ecology of *Ornithodoros P. tunicata americanus* MARX IXODOIDEA; ARGASIDAE and other commensal invertebrates present in the burrows of the gopher tortoise, *Gopherus polyphemus* DAUDIN. Ph.D.dissertation. University of Florida, Gainesville. 277 pp.

Moler, P.E. 1992. Rare and endangered biota of Florida. Volume III. Amphibians and reptiles. University Press of Florida, Gainesville, FL., 291 pp.

Moroka, N., R. Beck, and R. Pieper. 1982. Impact of burrowing activity of the banner-tail kangaroo rat on southern New Mexico desert rangelands. *Journal of Range Management*, 35:707-710.

Morton, S. R., and R.E. MacMillen. 1982. Seeds as sources of preformed water for desert-dwelling granivores. *Journal of Arid Environments*, 5:61-67.

Mushinsky, H.R., and L.A. Esman. 1994. Perceptions of gopher tortoise burrows over time. *Florida Field Naturalist*, 22 1: 1-28.

Mushinsky, H.R., and E.D. McCoy. 1995. Vertebrate species composition of selected scrub island on the Lake Wales Ridge of Central Florida. Nongame Wildlife Program Final Report Number NG87-149. Florida Game and Fresh Water Fish Commission, Tallahassee.

Myers, J.H. 1978 Selecting a measure of dispersion. *Environmental Entomology* 7:619-621.

Myers, R. 1990. Scrub and high pine. In: Myers, R. and Ewel, J. (eds.), *Ecosystems of Florida*, pp. 150-193. University of Central Florida Press, Orlando. 765 pp.

Nagy, K.A., and M.J. Gruchacz. 1995. Seasonal water and energy metabolism of the desert-dwelling kangaroo rat *Dipodomys merriami*. *Physiological Zoology*, 67: 1461-1478.

Naumov, N.P., and V.S. Lobachev. 1975. Ecology of desert rodents of the USSR: Jerboas and Gerbils, Pp 465-598 In: Prakash, I. and P.K. Ghosh. (eds), *Rodents in desert environments*, Dr. W. Junk Publishers, The Hague. 624 pp.

Neill, W.T. 1952. The spread of the armadillo in Florida. *Ecology* 33: 283-284.

Newman, C.M. 1997. The Florida Mouse (*Podomys floridanus*): long-term dynamics of a population in the high pine sandhills of Putnam County, Florida. M.S. Thesis. University of Florida, Gainesville.

Nichols, J.D., and M.J. Conroy. 1996. Techniques for estimating abundance and species richness. Pp 177-234 In: D.E. Wilson, F.R. Cole, J.D. Nichols, R.Rudran, and M.S. Foster

- (eds.) Measuring and monitoring biological diversity: standard methods for mammals. Smithsonian Institution Press, Washington, D.C., USA. 409 pp.
- Nichols, J.D., T. Boulinier, J.E. Hines, K.H. Pollock, and J.R. Sauer. 1998a. Inference methods for spatial variation in species richness and community composition when not all species are detected. *Conservation Biology* 12:1390-1398.
- Nichols, J.D., T. Boulinier, J.E. Hines, K.H. Pollock, and J.R. Sauer. 1998b. Estimating rates of local species extinction, colonization and turnover in animal communities. *Ecological Applications* 8:1213-1225.
- O'Farrell, M.J., W.A. Clark, F.H. Emmerson, S.M. Juarez, F.R. Kay, T.M. O'Farrell, and T.Y. Goodlett. 1994. Use of a mesh live trap for small mammals: are results from Sherman live traps deceptive? *Journal of Mammalogy* 75:692-699.
- Olsen, E., and K. Bolles. 1975. Permo-carboniferous fresh water burrows. *Fieldiana Geology*, 33 15: 271-290.
- Otis, D.L., K.P. Burnham, G.C. White, and D.R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62:1-135.
- Overton, W.S. 1971. Estimating the numbers of animals in wildlife populations. Pp. 403-456. In R.H. Giles (ed.) *Wildlife Management Techniques*. third edition. The Wildlife Society, Washington, DC. 633 pp.
- Parer, I., P.J. Fullagar, and K.W. Malafant. 1987. The history and structure of a large warren of the rabbit, *Oryctolagus cuniculus*, at Canberra, A.C.T. *Australian Wildlife Research*, 14: 505-513.
- Paton, T.R., and G.S. Humphreys. 1995. *Soils: A new global view*. New Haven, CT: Yale University Press. 201 pp.
- Pearson, P.G. 1955. Population ecology of the Spadefoot Toad, *Scaphiopus h. holbrooki* Harlan. *Ecological Monographs* 25:233-267.
- Pfeifer, S.L. 1980. Demographic and behavioral influences on juvenile Wyoming Ground squirrel dispersal. PhD. Dissertation, University of Colorado, Boulder, CO. 160 pp.
- Pielou, E.C. 1969. *Introduction to mathematical ecology*. Wiley-Interscience, New York, NY. 286 pp.
- Platt, S.G., T.R. Rainwater, and S.W. Brewer. 2004. Aspects of the burrowing ecology of nine-banded armadillos in northern Belize. *Mammalian Biology*, 69(4):217-224.

- Polis, G.A., C. Myers, and M. Quinlan. 1986. Burrowing biology and spatial distribution of desert scorpions. *Journal of Arid Environments*, 10:137-146.
- Pollock, K.H. 1982. A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:757-760.
- Pollock, K.H., J.D. Nichols, T.R. Simons, G.L. Farnsworth, L.L. Bailey, and J.R. Sauer. 2002. Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics* 13:105-199.
- Pough, F., D. Morafka, and P. Hillman. 1978. The ecology and burrowing behavior of the Chihuahuan fringe-footed lizard, Uma exsul. *Copeia*, 1: 81-86.
- Power, M.E., Tilman, D, Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G, Castilla, J.C., Lubchenco, J., and Paine, R. 1996. Challenges in the Quest for Keystones. *BioScience*, 468:609-620.
- Prakash, I. 1997. Ecology of desert mammals. *Current Science*, 721:31-34.
- Randall, J.A., and E.R. Lewis. 1997. Seismic communication between the burrows of kangaroo rats, Dipodomys spectabilis. *Journal of Comparative Physiology A*, 181:525-531.
- Rogovin, K.A., E.J. Heske, and G.I. Shenbrot. 1996. Patterns of spatial organization and behavior of Pygeretmus pumilio Kerr, 1792 Dipodidae, Rodentia: radiotelemetry study in the Dagestan desert, Russia. *Journal of Arid Environments*, 33:355-366.
- Reichman, O.J., and S.C. Smith. 1990. Burrows and burrowing behavior by mammals. In: Genoways, H.H. (ed.), *Current Mammalogy*, Volume 2, pp. 197-244. New York, NY: Plenum Press. 596 pp.
- Resetar, A., and H. Marx. 1981. A redescription and generic reallocation of the African colubrid snake Elapocalamus gracilis Boulenger with a discussion of the union of the brille and postocular shield. *Journal of Herpetology*, 151:83-89.
- Reynolds, T.D., and J.W. Laundre. 1988. Vertical distribution of soil removed by four species of burrowing rodents in disturbed and undisturbed soils. *Health Physics*, 54: 445-450.
- Reynolds, T.D., and W.L. Wakkinen. 1987. Characteristics of the burrows of four species of rodents in undisturbed soils in southeastern Idaho. *The American Midland Naturalist*, 118: 245-250.
- Rogovin, K.A., E.J. Heske, and G.I. Shenbrot. 1996. Patterns of spatial organization and behavior of Pygeretmus pumilio Kerr, 1792 (Dipodidae, Rodentia): radiotelemetry study in the Dagestan desert, Russia. *Journal of Arid Environments*, 33:355-366.

Rumke, C.L. 1975. Implications of the statement: no side effects were observed. *The New England Journal of Medicine* 2927: 372-373.

Salmon, T.P., R.E. Marsh, and D. Stroud. 1987. Influence of burrow destruction on recolonization by California ground squirrels. *Wildlife Society Bulletin*, 15: 564-568

Schmalzer, P.A., M.A. Hensley, and C.A. Dunlevy. 2001. Background characteristics of soils of Kennedy Space Center, Merritt Island, Florida: selected elements and physical properties. *Florida Scientist* 64(3):161-187.

Schoener, T.W. 1987. The geographical distribution of rarity. *Oecologia Berlin*, 74: 161-173

Schropfer, R., and B. Klenner-Fringes. 1991. Minimizing interspecific competition by different foraging strategies in two North African desert rodents. *Acta Theriologica*, 361-2: 109-117.

Senzota, R.B.M. 1984. The habitat, abundance and burrowing habits of the gerbil, Tatera robusta, in the Serengeti National Park, Tanzania, *Mammalia* 482:185-195.

Sheets, R.G., R.L. Linder, and R.B. Dahlgren. 1971. Burrow systems of prairie dogs in South Dakota. *Journal of Mammalogy* 52:451-453.

Shenbrot, G.I., Krasnov, B.R. and Khokhlova, I.S. 1997. Biology of Wagner's gerbil Gerbillus dasyurus Wagner, 1842 Rodentia: Gerbillidae in the Negev Highlands, Israel. *Mammalia*, 614: 467-486.

Sherman, H.B. 1936. A list of the recent land mammals of Florida. *Proceedings of the Florida Academy of Science* 1:102-128

Shump, K.A., Jr. 1976. Ecological importance of nest construction in the hispid cotton rat *Sigmodon hispidus*. PhD. Dissertation, Michigan State University, East Lansing, MI. 106 pp.

Simons, L.H. 1991. Rodent dynamics in relations to fire in the Sonoran Desert. *Journal of Mammalogy*, 723: 518-524.

Smith, A.P., and D.G. Quin. 1996. Patterns and causes of extinction and decline in Australian Conilurine rodents. *Biological Conservation* 77: 243-267.

Smith, B.E. 2006. A problem with Amphibian calling surveys: not all species are equally observable. North American Amphibian Monitoring Program, Calling-Amphibian Surveys. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD.
<http://www.pwrc.usgs.gov/naamp3/papers/37ss.html>

Smith, R.B., T.D. Tuberville, A.L. Chambers, K.M. Herpich, and J.E. Berish. 2005. Gopher tortoise burrow surveys: external characteristics, burrow cameras, and truth. *Applied Herpetology* 2:161-170.

Smithers, R.H.N. 1971. The mammals of Botswana. Museum Memoir No. 4. Salisbury, Rhodesia: The Trustees of the National Museums of Rhodesia, 340 pp.

Smith-Gill, S.J. 1975. Cytophysiological basis of disruptive pigmentary patterns in the leopard frog Rana pipiens. II Wild type and mutant cell specific patterns. *Journal of Morphology* 146:35-54.

Sokal, R.R., and R.J. Rohlf. 1981. *Biometry*. second edition. Freeman. San Francisco, CA. 859 pp.

Speake, D. 1981. The gopher tortoise community. In: Lohofener, R, Lohmeier, L. and Johnson, G. (eds.), *The future of gopher tortoise habitats*. Proc. 2nd annual meeting, Gopher Tortoise Council, pp 44-47. Gainesville, FL: Florida State Museum. 86 pp.

Steel, R.G.D., and J.H. Torrie. 1980 *Principles and procedures of statistics: a biometrical approach*. second edition. McGraw-Hill Book Company, New York. 633 pp.

Steiniger, F. 1949. Biologische Beobachtungen an freilebenden Wanderratten auf der Hallig Norderog. *Verhandl. Deutsch, Zool*, 152-156.

Steiniger, F. 1950. Beitrage zur Soziologie und sonstigen Biologie der Wanderratte. *Z. Tierpsychologie*, 7: 356-379.

Steiniger, F. 1952. *Rattenbiologie und Rattenbekämpfung*. Stuttgart: Ferdinand Enke. 149 pp.

Stone, E., and N.B. Comerford. 1994. Plant and animal activity below the solum. *Whole regolith pedology* No. 34. Madison, WI.:Soil Science Society of America. 20 pp.

Stott, P. 1996. Ground-penetrating radar: a technique for investigating the burrow structures of fossorial vertebrates. *Wildlife Research* 23:519-30.

Stromberg, M.R. 1978. Subsurface burrow connections and entrance spatial pattern of prairie dogs. *Southwestern Naturalist*, 232: 173-180.

Sutherland, W.J. 1996. *Ecological census techniques: A handbook*. Cambridge University Press, Cambridge, UK. 336 pp.

Taber, F.W. 1945. Contribution on the life history and ecology of the nine-banded armadillo. *Journal of Mammalogy* 26:211-226.

Taub, F.B. 1961. The distribution of the red-backed salamander, Plethodon c. cinereus, within the soil. *Ecology* 42:681-698.

- Taulman, J.F., and L.W. Robbins. 1996. Recent range expansion and distributional limits of the nine-banded armadillo Dasypus novemcinctus in the United States. *Journal of Biogeography* 23: 634-648.
- Taylor, W.P. 1935. Some animal relations to soils. *Ecology*, 16: 127-136.
- Thompson, S.K. 2002. *Sampling*. John Wiley and Sons, Inc. New York. 400 pp.
- Thompson, W.L, G.C. White, and C. Gowan. 1998. *Monitoring vertebrate populations*. Academic Press, Inc. San Diego, 365 pp.
- Thorp, J. 1941. Effects of certain animals that live in soils. *Science Monthly*, 68: 180-191.
- Tognelli, M.F., C. M. Campos, R.A. Ojeda, and V.G. Roig. 1995. Is Microcavia australis Rodentia: Caviidae associated with a particular plant structure in the Monte desert of Argentina? *Mammalia*, 59: 327-333.
- Tuberville, T.D. 1998. Effects of soil disturbance by gopher tortoises Gopherus polyphemus on vegetation structure and composition in a pine-oak sandhills community. M.S. Thesis. University of Georgia, Athens, Georgia.
- Turner, L. 1972. Autecology of the Belding Ground Squirrel. PhD. dissertation, University of Arizona, Phoenix, AZ. 166 pp.
- van Aarde, R.J., Willis, C.K., Skinner, J.D. and Haupt, M.A. 1992. Range utilization by the aardvark, Orycteropus afer Pallas, 1766 in the Karoo. *South Africa*, 22:387-394.
- van Heerden, J., and Dauth, J. 1985. Aspects of adaptation to an arid environment in free-living ground squirrel, Xerus inauris. *Journal of Arid Environments*, 13: 83-89
- Vander Wall, S. 1990. *Food hoarding in animals*. University of Chicago Press, Chicago, IL. 445 pp.
- Vlasov, Y. 1937. The burrow as a particular biotope in the vicinity of Ashkhabad In Russian. In: *Problems of the parasitology and fauna of Tirkmenia*. Press of the USSR Academy of Sciences, pp. 223-240. Moscow-Leningrad. Original not seen, quoted from Krivokhatskiy, V. undated Repetek Sand-Desert Station and Reserve, Institute of Deserts, USSR Academy of Science.
- Waddell, B.J. 1986. The effects of patch area, isolation, and habitat quality on the distribution and dispersion of Columbian ground squirrels Spermophilus columbianus in meadow steppe. PhD. dissertation, Washington State University, Pullman, WA. 369 pp.

- Walker, E.P. 1968 (ed.) Mammals of the World, second edition. Baltimore: Johns Hopkins University Press, 1629 pp.
- Walther, B.A., and S. Morand. 1998. Comparative performance of species richness estimation methods. *Parasitology* 116:395-405.
- Watts, C.H.S. 1995. Plains Rat Pseudomys australis. In: Strahan, R. (ed.), Mammals of Australia, pp.585-587. Washington: Smithsonian Institution Press. 756 pp.
- Webb, S.D. 1990. Historical Biogeography. Pp 70-100 In: R.L. Myers and J.H.J. Ewel (eds.) Ecosystems of Florida. University of Central Florida Press, Orlando.765 pp.
- Weiss, N.T., and B.J. Verts. 1984. Habitat and distribution of pygmy rabbits Sylvilagus idahoensis in Oregon. *Great Basin Naturalist*, 44: 563-571.
- Whicker, A.D., and J.K. Detling. 1988. Ecological consequences of prairie dog disturbances. *BioScience*, 38 11: 778-785.
- Whitaker, J.O., Jr. 1992. The Audubon Society Field Guide to North American Mammals. Alfred Knopf, Inc. New York 745 pp.
- White, G.C., and L.E. Eberhardt. 1980. Statistical analysis of deer and elk pellet-group data. *Journal of Wildlife Management*. 44:121-131.
- White, G.C., and R.E. Bennetts. 1996 Analysis of frequency count data using the negative binomial distribution. *Ecology* 77:2549-2557.
- White, W.A. 1970. The geomorphology of the Florida peninsula. Florida Department of Natural Resources. Geological Bulletin Number 51, Tallahassee, FL.
- Wilcomb, M.J. 1954. A study of prairie dog burrow systems and the ecology of their arthropod inhabitants in central Oklahoma. PhD. dissertation, University of Oklahoma, Norman, OK. 158 pp.
- Williams, B.K., J.D. Nichols, and M.J. Conroy. 2001 Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press. San Diego.817 pp.
- Williams, D.A. 1976. Improved likelihood ratio tests for complete contingency tables. *Biometrika* 63:33-37.
- Wilson, D.S., H.R. Mushinsky, and E.D. McCoy. 1991. Relationship between gopher tortoise body size and burrow width. *Herpetological Review*, 22 4: 122-124.
- Wirtz, W.O., D.H. Austin, and G.W. Dekle. 1985. Food habits of the common long-nosed armadillo Dasypus novemcinctus in Florida, 1960-61. Pp. 439-451 In: G.G. Montgomery

(ed.) The evolution and ecology of Armadillos, Sloths, and Vermilinguas. Smithsonian Institution Press, Washington. 451 pp.

Witz, B.W., D.S. Wilson, and M.D. Palmer. 1992 Estimating population size and hatchling mortality of Gopherus polyphemus. Florida Scientist 55:14-19.

Wood, D.A. 1996. Florida's endangered species, threatened species, and species of special concern. Official Lists. Florida Game and Fresh Water Fish Commission, Tallahassee, FL 14 pp.

Woodbury, A.M., and R.Hardy. 1948. Studies of the desert tortoise, Gopherus agassizii. Ecological Monographs, 18:145-200.

Yensen, E., D. Quinney, K. Johnson, K. Timmerman, and K. Steenhof. 1991. Fire, vegetation changes, and population fluctuations of Townsend's ground squirrels. American Midland Naturalist, 128: 299-312.

Yoccoz, N.G., J.D. Nichols, and T. Boulinier. 2001. Monitoring of biological diversity in space and time. Trends in Ecology and Evolution 16:446-453.

Young, P.J. 1990. Structure, location and availability of hibernacula of Columbian ground squirrels Spermophilus columbianus. American Midland Naturalist, 123: 357-364.

Zielinski, W.J., R.L. Truex, C.V. Ogan, and K. Busse. 1997. Detection surveys for fishers and American martens in California, 1989-1994: summary and interpretations. Pp 172-392 In: G. Proulx, H.N. Bryant, and P.M. Woodard eds Martes: taxonomy, ecology, techniques, and management. Provincial Museum of Alberta, Edmonton, Alberta, Canada.

Zimmerman, J.W. 1982. The common long-nosed armadillo Dasypus novemcinctus in northcentral Oklahoma. M.Sc. Thesis. Oklahoma State University, Stillwater, OK. 106 pp.

Zimmerman, J.W. 1990. Burrow characteristics of the nine-banded armadillo, Dasypus novemcinctus. The Southwestern Naturalist, 35 2: 226-227.

BIOGRAPHICAL SKETCH

Alton Emory Kinlaw was born in North Carolina and graduated from Rockingham High School. He attended the University of North Carolina at Chapel Hill and graduated with a Bachelor of Science degree in Pharmacy. Recognizing his long interest in the environment, he began taking wildlife courses as a post-baccalaureate student at North Carolina State University and the University of Georgia. He then attended the University of Idaho, where he received a Bachelor's in Wildlife-Fisheries Resources. He returned to North Carolina State University and completed a Master's Degree in Wildlife Biology, working on a self-funded project involving capture-recapture of spotted skunks at Canaveral National Seashore, Florida. During all academic pursuits, including the University of Florida, he has worked full time as a hospital pharmacist and funded a large portion of his own research. He is married to Monnie Kinlaw, with one daughter, Skye.