

URBAN FOX SQUIRREL ECOLOGY AND MANAGEMENT

A Dissertation

by

ROBERT ALAN MCCLEERY

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2007

Major Subject: Wildlife and Fisheries Sciences

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ABSTRACT

Urban Fox Squirrel Ecology and Management.

(May 2007)

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Chair of Advisory Committee: Dr. Roel R. Lopez

I studied the habitat selection, survival, and anti-predator behaviors of the fox squirrel (*Sciurus niger*) across the urban-rural gradient in College Station, Texas. From two years of tracking the radio locations of 82 fox squirrels, my data suggested that fox squirrels in urban areas selected for use large mast bearing trees that mimicked the habitat features they prefer in non-urban areas and avoided conifer and ornamental tree species. Urban fox squirrels selected to use buildings and non-native grass during certain seasons and showed a tolerance for pavement, including it proportionally in their core-areas. Analysis of radio-telemetry data of urban and rural fox squirrels suggested that the rates of survival and causes of mortality differed between the two populations. At least 60% of the mortalities on the rural site were caused by predation, while < 5% of the mortalities on the urban site were caused by predation. Most of the mortalities on the urban site (>60%) were caused by vehicular collisions. Observations of anti-predator behaviors supported my hypothesis that squirrels decrease their anti-predator behaviors as the human presence increases. Observational data also supported my hypothesis that this phenomenon was caused by habituation. I also found that the time dedicated to anti-predator behaviors differed among urban, rural, and suburban fox squirrel populations in

response to coyote and hawk vocalizations. The mean responses to both vocalizations on the rural site (coyote = 45%, hawk = 55%) were at least twice that of those found on the urban sites (coyote = 11%, hawk = 20%). I also used survey responses to questions about squirrel management to test theoretical frameworks linking attitudes to behaviors. My data suggests that beliefs and attitudes that are modified by variables shown to increase accessibility generally correspond better to behaviors. My data also suggests that the inclusion of a measure of previous behaviors will increase the predictive ability of models within different theoretical frameworks. Most importantly for the advancement of a comprehensive theoretical framework, my study showed that composite models combining components of the theory of reasoned action and attitude to behavioral process models out-performed other models.

DEDICATION

Amanda

Thank for the love, joy, and support you have given me

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The idea and logistical foundation for this research was provided by Roel Lopez. Thank you Roel for giving me the freedom to succeed as researcher and for the giving me the independence to pursue my own interests. I value your advice on matters both professional and personal and I am proud to consider you a good friend. Dr. Silvy, from the day I came to College Station 6 years ago you have always gone out of your way to make sure I felt at home in College Station. Thank you for your guidance, advice, support, friendship, and belief in me as a researcher, teacher and a person. Jane Sell, thank you for helping to shape my views of social research and for giving me your time and expertise for my attitudinal research. Dr. Grant and Dr. Slack your support and insight have been invaluable to this project and throughout my graduate career. Thank you.

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CHAPTER I

INTRODUCTION

Background

Over the next 100 years the planet is expected to continue its unprecedented 200-year alteration from rural to urban landscapes (Adams et al. 2005). As the planet's landscape has changed, some wildlife species have struggled (mostly specialists) to adapt and survive while others have thrived (mostly generalists) in highly altered urban environments (Adams et al. 2006). Some mammal species such as squirrels (*Sciurus* spp.), white-tailed deer (*Odocoileus virginianus*), raccoons (*Procyon lotor*), and coyotes (*Canis latrans*) have acclimated to urban and suburban landscapes (McShea et al. 1997, Mosillo et al. 1999) providing urbanities the opportunities and responsibilities of living within close proximity to wildlife. This new, potentially rewarding and potentially dangerous, interface of people and wildlife in urban environments must be understood to foster an environment that is conducive to humans and wildlife alike.

Limited research suggests that wildlife species that have adapted to urbanized environments have shown changes in their population dynamics, behavior, movements, and habitat selection (VanDruff et al. 1996) relative to their rural counterparts. Nonetheless, there is lack of information about the ecology of many common wildlife species in urban environments. This lack of information makes it difficult for managers

of urban wildlife populations to make ecologically sound decisions (VanDruff et al. 1996).

Urban wildlife also differs from rural wildlife in another important way. Unlike in isolated rural areas, urban species live in direct proximity to humans with whom they are in increased contact and conflict. As a consequence, the effective management of urban wildlife also requires an understanding of the behaviors and attitudes of the human inhabitants surrounding these wildlife populations (Adams et al. 2005).

Fox squirrels (*S. niger*) are common, easily recognizable (Gilbert 1982), and highly visible in many urban areas. Urbanites hold various opinions of squirrels conversely finding them a desirable species around the home (Brown et al. 1979, Gilbert 1982) and a nuisance (Conover 1997). In spite of public sentiment to increase or sometimes decrease squirrel populations in urban settings, there is only limited information on urban tree squirrel ecology (Williamson 1983, VanDruff and Rowse 1986, McPherson and Nilon 1987, Salisbury et al. 2004) to aid managers in the manipulation of urban squirrel populations. The effective management of squirrels and other urban wildlife populations can be enhanced considerably by studying them in an urban landscape and understanding how they have adapted to human dominated environments (Loker et al. 1999). For example, understanding what habitats and habitat features urban squirrels select would allow managers to consider increasing or removing these features as necessary, and knowing the causes of urban squirrel mortality would allow managers to consider fostering or removing factors that limit squirrel population size.

Study Area

I conducted research on 3 sites chosen to represent urban, suburban, and rural areas on an urban-rural gradient. The center or urban area of the gradient was represented by 140 ha of the main campus of Texas A&M University in College Station, Texas, USA. Over 45,000 students attended the university during the study and there was a nearly constant flow of pedestrians and vehicles on the campus. The site was comprised of a dense nucleus of buildings, parking lots and streets. Extending out from this nucleus was an area of courtyards like configurations of buildings. Some of the dominant trees species found on the study site were live oak (*Quercus fusiformis* and *Q. virginiana*), post oak (*Q. stellata*), Bradford pear (*Pyrus calleryana*), arborvitae (*Thuja* spp.), and elm (*Ulmus* spp.).

To represent the rural end of the urban-rural gradient I conducted squirrel behavioral observations on a private ranch 18-km from the urban site. The ranch was surrounded by other ranches and bordered by the Navasota River. The portion of the ranch used for research was approximately 240 ha of undisturbed bottomland hardwood forest and meadows that had little to no human activity on it. Squirrels had not been hunted or fed on this site for at least 30 years. Some of the dominant trees species on the site included post oak (*Q. stellata*), water oak (*Q. nigra*), pecans (*Carya* spp.), and elms.

The suburban study site was chosen to represent the middle of the urban-rural gradient. The study site was comprised of 15 suburban parks ranging in size from 10–112 ha. These parks were located on the periphery (5–10 km from the urban site) of the

city of College Station, Texas, USA and had a variety of landscapes, but were mostly dominated by oaks (*Q. spp*) with open under stories and grass fields. These parks varied in their rates of human visitation (averaging 32 visitors daily), but all the parks had considerably less human activity than the urban site and considerably more human activity than the rural-study site.

Objectives

The purpose of this study was to observe fox squirrel ecology and behavior in urban settings and to compare differences between urban and rural squirrel populations. Additionally, I used the fox squirrel to present and test a new model for assessing reactions to potentially controversial management decisions made for the management of urban wildlife. The objectives of the study were to:

1. Discern how fox squirrels use the biotic and abiotic features common to all urban environments on different scales.
2. Determine the differences in survival and mortality between rural and urban fox squirrels for each sex and season.
3. Investigate the differences in anti-predator behaviors and responses to humans among urban, suburban and rural fox squirrel populations.
4. Construct and test a theoretical framework to more effectively predict stakeholders' behaviors from their attitudes, experiences, norms, and knowledge.

CHAPTER II

HABITAT SELECTION

Synopsis

Tree squirrels are one of the most familiar mammals found in urban areas and conversely considered to be desirable around homes at times and a pest at other times. I examined fox squirrel (*Sciurus niger*) habitat use in inner city and suburban areas using radio telemetry. Habitat selection ratios were estimated at differing scales by season and fox squirrel activity. Telemetry data suggests those radio-collared fox squirrels ($n = 82$) preferentially selected areas: with greater tree canopy, that contained live oaks (*Quercus fusiromis* and *Q. virginiana*) and with trees of large diameters and canopies during periods of inactivity. Fox squirrels also preferred to use the inside of buildings within their core areas during the winter and spring when inactive, and grassy areas during periods of activity in the fall and spring. During periods of activity, fox squirrels avoided using pavement but did not exclude it from their core area movements. Their ability to tolerate pavement in core area movements and to use buildings made vast areas of the urban environment available for fox squirrels to exploit. I found that the number of large and medium trees, amount of pavement and grassy areas, canopy cover, number of oaks, and the area covered by buildings were all important factors in predicting fox squirrel activity in an urban environment.

Introduction

In the twenty-first century, natural landscapes are expected to continue their unprecedented 200-year alteration from rural to urban landscapes (Adams et al. 2006). Wildlife managers and scientists are attempting to prepare for these changes; however, there is only a cursory understanding of and limited body of literature available on wildlife management in urban areas (Wolch et al. 1995, VanDruff et al. 1996, Adams et al. 2005, Adams et al. 2006). Some wildlife populations, such as deer, squirrels, and geese have managed to adjust to human-dominated landscapes by modifying their basic ecology through a process defined as synurbanization (Adams et al. 2005). This adjustment of wildlife populations to urbanization, or synurbanization, usually leads to changes in population size, sex/age structure, survival, behavior, and habitat use (Gliwicz et al. 1994), making it ineffectual to manage urban populations with research conducted on wildlife populations in rural settings. Nonetheless, there is a lack of information even on the basic ecology of common wildlife species inhabiting urban areas. For simplicity, I defined these urban areas as places of relatively dense human population, where most of the land is dedicated to buildings, concrete, grassy lawns, and other human uses (Adams et al. 2006).

Tree squirrels (*Sciurus* spp.) are highly visible in urban areas of North America where residents consider them to be one of the biggest pests, and conversely, desirable around their homes (Brown et al. 1979, Gilbert 1982, Conover 1997, Adams et al. 2006). Nonetheless, there is still much to be learned (Williamson 1983, VanDruff and Rowse 1986, McPherson and Nilon 1987, Salisbury et al. 2004) about the use of urban habitats,

especially by the fox squirrel (*S. niger*), a common tree squirrel found in cities throughout the mid-west (Adams 1994) and southern (Flyger 1974) United States. To the best of my knowledge, only 1 study has examined urban habitat use by fox squirrels in fragmented wood lots (Salisbury et al. 2004), and I am not aware of any studies of fox squirrels' usage of the biotic and abiotic substrates commonly found in inner city and suburban areas. Wildlife managers, urban planners, animal damage control officials, homeowners, and squirrel enthusiasts could use such habitat information to attract or manage fox squirrel populations through the manipulation of the urban environment.

In contrast to traditional habitat use studies that look strictly at the biotic environment (Kantola and Humphrey 1990, Lopez et al. 2004, Perkins and Conner 2004), I evaluated fox squirrels' interactions with the biotic and abiotic features unique to urban environments: buildings, planted and ornamental trees, concrete, and exotic manicured grasses (Adams 1994). My study objectives were to: (1) discern fox squirrel use of space in relation to the urban substrates, (2) determine tree characteristics selected by fox squirrels during periods of activity and inactivity, and (3) develop a model to determine which features in the urban environment affect levels of fox squirrel activity.

Methods

Study Area

Research was conducted on the Texas A&M University main campus (140 ha) in College Station, Texas. The campus was comprised of a diversity of urban habitats ranging from inner city areas to more typical suburban areas (Figure 2.1). The center of

the study area was covered with a dense nucleolus of buildings and parking lots. Extending out from this nucleolus was an area, comprised of widely spaced buildings interspersed with open fields and sparsely forested openings with no under story, characteristic of many parks and cemeteries in suburban areas (Adams 1994). The dominant tree species found on the study site were live oak (*Quercus fusiformis* and *Q. virginiana*), post oak (*Q. stellata*), Bradford pear (*Pryus calleryana*), arborvitae (*Thuja* spp.), and elm (*Ulmus* spp). Most species of trees found in my study site were commonly found in urban areas in Texas and throughout the southeastern United States (Gilman 1997). In addition, a unique aspect of my research was the complete geo-referencing or GIS (geographic information system) of the substrates (e.g., trees, sidewalks, buildings, etc.) found on the study site.



Figure 2.1. Depiction of geo-referenced urban substrates on the study site (Texas A&M University, College Station, Texas, USA) divided into 140 1-ha plots, from GIS (geographic information system) database.

Habitat Substrates

We categorized dominant habitat substrates within the study area into 4 major groups: pavement, buildings, grass and tree canopy. Habitat substrates were classified using 1-m digital-ortho quarter quads (DOQQs, from 2001) or obtained from an existing GIS database for the campus. For the building classification, there were 163 buildings within the study site, ranging from small storage sheds and green houses to 15-story buildings. This category accounted for 32 ha of the study area. The pavement classification consisted of all roads, parking lots, paved walkways, courtyards, and building entrances. Pavement was the most dominant feature within the study area and accounted for 54 ha of study area. The grass classification (46 ha) was comprised of all areas with manicured lawns and non-native grassland areas. And lastly, for the tree classification, a comprehensive GIS tree (>2 m in height) coverage was obtained that included tree species, canopy area, and diameter at breast height (DBH) for each individual tree on campus. Total tree canopy area within the study site was 22 ha; however, for data analysis, it is important to note that most of the canopy cover occurred over areas classified as pavement, grass, or buildings. As a result, substrates were measured on multiple planes accounting for >154 ha of total substrate area.

Trapping

We trapped fox squirrels from August 2003 through June 2005 in an effort to maintain a continuous sample of at least 20 fox squirrels (10 male, 10 female) with functioning radio-collars. To trap fox squirrels, I strapped >65 Tomahawk wire-cage

traps (No. 103, Tomahawk Live Trap Company, Tomahawk, Wisconsin, USA) to the limbs of trees (Korschgen 1981, Adams 1984), effectively covering the study area. Traps were pre-baited with sunflower seeds and pecans 2–3 days prior to trapping to increase trapping success. Once fox squirrels were captured they were sexed, aged (Dimmick and Pelton 1996), and weighed. For identification, each fox squirrel was ear-tagged (Monel 1005-3, National Band and Tag Company, Newport, Kentucky, USA) and a passive integrated transponder (PIT tag, Biomark, Boise, Idaho, USA) was injected subcutaneously prior to release (Korschgen 1981, Samuel and Fuller 1996). Captured adult fox squirrels that had the potential for reproductive activity (>7 months old) (McCloskey and Vohs 1971), were fitted with a collar and battery-powered mortality-sensitive radio transmitter (150-152 MHz, 12 g, model M170 Advanced Telemetry Systems, Isanti, Minnesota, USA or 10g, model MP-2 AVM Instrument Company, Colfax, California, USA).

Radio Telemetry

We tracked radio-collared fox squirrels from September 2003 through August 2005. I located fox squirrels 2–3 times per week at random intervals (16-hour periods divided into 8 equal 2-hour segments; one 2-hour segment was randomly selected and during that time all fox squirrels were located). I located fox squirrels via homing signals (White and Garrott 1990), noted their position on geo-referenced maps and recorded the habitat substrate (i.e., tree, grass, pavement, or building) occupied by the fox squirrel. If a fox squirrel was located in a tree, I recorded the tree's unique

identification number. I also recorded the fox squirrel's activity to differentiate between the fox squirrel's selection of day time refugia (e.g., areas used for shelter) and selection of habitat features during activity periods (e.g., foraging, mating, grooming, etc.) (McCloskey 1975). All locations and information were entered into the GIS database.

Data Analysis

We evaluated fox squirrel habitat use at multiple spatial and temporal scales. Evaluating habitat use at different spatial scales can help reduce the biases introduced by defining what habitats are available to individual animals or animal populations (Porter and Church 1987). In total, I evaluated fox squirrel habitat selection on 5 spatial scales during different times of the year and distinct behavioral states. I used habitat selection ratios (the observed portion of habitat used divided by the portion of habitat expected to be used) (Manly et al. 2000, Lopez et al. 2004), for the first 3 spatial scales, which analyzed fox squirrel use of urban substrates. Habitat selection ratios were calculated by season (fall = 22 September to 21 December, winter = 22 December to 21 March, spring = 22 March to 21 June, summer = 22 June to 21 September) to reduce the temporal biases (Anderson and Gutzwiller 1996). I combined male and female estimates by season, as a result of the small sample sizes and because previous studies have reported that fox squirrels do not differentially use habitat by sex (Perkins and Conner 2004). Finally, I incorporated a behavioral component, or scale to the analysis. Fox squirrels can be inactive for large portions of the day (Hicks 1949), especially during summer and winter. Separating the analysis of fox squirrel substrate use by activity and inactivity

minimized potential biases due to fox squirrel behavior. A description of each of the scales used is provided below.

Point-study area-We examined fox squirrel habitat selection on a point-study area scale (comparable to Johnson's (1980) first order selection). I calculated habitat-selection ratios (S) for each fox squirrel by dividing observed use by expected use for each substrate and season. Selection ratios were calculated as $S = u / (n_x * p_h)$, where u = the number of radio locations on a substrate for an individual, n_x = the total number of radio locations for an individual and p_h = the portion of substrate for the entire study area (Aebischer et al. 1993, Lopez et al. 2004).

Range-study area-We evaluated range selection of fox squirrels by comparing the proportions of substrates within a given fox squirrel's range to the proportions of substrates on the study area (comparable to Johnson's (1980) second order selection). Habitat selection ratios were calculated for each fox squirrel as $S = p_r / p_h$, where p_r = the portion of substrate inside an individual's range and p_h = the portion of substrate for the entire study area.

Point-range-We evaluated fox squirrel habitat selection within an animal's range (comparable to Johnson's (1980) third order selection). I compared the number of fox squirrel locations on a given substrate to the proportional amount of that substrate available within each fox squirrel's range. More specifically, I determined habitat selection ratios as $S = u_r / (n_t * p_r)$, where u_r = the number of radio locations on a substrate for an individual within its range, n_t = an individual's total number of radio locations inside its range, and p_r = the portion of substrate inside an individual's range.

When calculating range-study area and point-range selection, it is common to represent animal ranges using 95% or 100% minimum convex polygons (MCPs) (Lopez et al. 2004, Perkins and Conner 2004). I chose to represent fox squirrel ranges using 50% kernels (Seaman et al. 1998) to yield a more precise estimate of the areas used by fox squirrels (i.e., 50% core area, hereafter “range”). Fox squirrels are not territorial and can have expansive MCP ranges (>40 ha) (Koprowski 1994) that encompass long distance travels (Kantola and Humphrey 1990). I calculated seasonal core areas as 50% kernels using animal movement extension (Hooge and Eichenlaub 1999) in ArcView 3.2. Only fox squirrels with over ≥ 30 telemetry locations per season (Seaman et al. 1999) were used in the calculation of range areas. Although the fox squirrel is one of the least arboreal tree squirrels (Conner and Godbois 2003), they still spend a considerable portion of their time in the tree canopy (Geeslin 1970). To adjust for this, I calculated the total area of ranges and the study site as a 2-planed total area (total area = the 2-dimensional area on the ground + 2-dimensional area encompassed by the tree canopy). Proportions of study site and range substrate areas were calculated as the area of the substrate divided by the 2 planed total area. In the calculation of selection ratios, I avoided zeros in the numerator or denominator by adding 0.01 to observed and expected values ($S = [U + 0.01] / [E + 0.01]$) (Aebischer et al. 1993, Lopez et al. 2004). Selection ratios > 1 suggest that animals used (i.e., preferred or selected) (Litvaitis et al. 1996) the substrate more frequently than expected while ratios < 1 suggest avoidance of the substrate (Manly et al. 2000).

Tree selection-For the fourth spatial scale, I examined fox squirrel use of trees in urban areas. In a manner similar to the examination of urban substrates, I partitioned fox squirrel telemetry data into periods of activity and inactivity. This micro level habitat analysis was comparable to Johnson's (1980) fourth order selection. I was in a unique position to conduct an analysis of tree level selection because of a comprehensive GIS tree database for the campus. From the database I could compare the species, canopy, and DBH of all trees where a squirrel was found to the species, canopy, and DBH of all trees on the study site in which a squirrel was not found. Due to the diversity of trees (>60 species) and minimal numbers of some tree species, I analyzed fox squirrel selection of only major tree groups within the study area. The 10 most numerous tree species and/or groups (>60 individuals) were: live oak, post oak, other oaks (*Quercus* spp.), pines (*Pinus* spp.), elms, Chinese pistachio (*Pistacia chinensis*), bald cypress (*Taxodium distichum*), arborvitae, Bradford pear (dominant large tree species), and other less dominant smaller fruit trees (*Malus* spp. and *Prunus* spp.).

To describe fox squirrels' use of trees by species, I compared the proportion of fox squirrel locations we expected to find in a particular species of tree (or group of trees) to the 95% CI of the proportion of fox squirrel locations observed in each species of tree. I calculated expected proportions ($E = T/W$, where E = expected fox squirrel use of a tree species) as the number of trees of a particular species (T) divided by the total number of trees on the study area (W). The proportion of observed fox squirrels ($O = L/T$, where O = observed use) was calculated as the number of fox squirrel locations recorded on each species of tree (L) divided by the total number of times fox squirrels

were located in trees (T). I compared, observed, and expected proportions with Wald binomial confidence intervals (Simonoff 2003) and compared the mean and 95% CI of the DBH and tree canopy between trees with fox squirrel locations (active and inactive) and trees with no squirrel locations recorded.

Squirrel activity-To discern which habitat components of the urban environment increased or decreased fox squirrel activity, I divided the study site in 140 1-ha grids and recorded every fox squirrel location within that grid over the 2-year period. Within each grid, I quantified 8 habitat components that I believed would affect fox squirrel activity: (1) the number of trees (*ntrees*), (2) the area of grass (*grass*), (3) the area of buildings (*build*), (4) the area of concrete, asphalt, and brick on the ground (*pave*), (5) the number of medium sized trees, DBH 14–20 cm (*medium*), (6) the number of large sized trees, DBH >20 cm (*large*), (7) the number of oaks (*oaks*), and (8) the area covered by canopy (*canopy*, the natural log of this value was used to better fit the model). I limited the number of *a priori* models to minimize over-fitting the data (Norman et al. 2004). The *a priori* models were generated from the limited urban tree squirrel habitat literature and field observations. I ran general linear model regressions of these models against the number of fox squirrel locations per grid fitted to a negative binomial distribution using SAS Institute (1999) (PROC GENMOD). First, I evaluated 8 *a priori* models, a global model containing all 8 variables (Model 10), and an intercept only model (Model 1) using Akaike's Information Criterion corrected for small sample size (AICc) (Simonoff 2003). From the evaluation of the *a priori* models, I generated a second set of *a posteriori* models (Models 11–16) (Norman et al. 2004). I tested the second set of

models and used the relative difference to the smallest AIC value in the entire set of models ($\Delta AICc$) and Akaike weights (w_i) to select the best approximating models (Burnham and Anderson 1998). I considered models with values of ≤ 4 AICc units to compete with the best model while models with values of > 4 AICc units were disregarded as an unlikely representation of the data (Burnham and Anderson 1998, Norman et al. 2004). To deal with the possibility of model uncertainty caused by competing models ≤ 4 AICc units from the model with the lowest AICc, I presented averaged model parameters and averaged 95% confidence intervals (Burnham and Anderson 1998).

Results

We collected 3,467 radio locations from 82 fox squirrels (42 males, 40 females) between August 2003 to 2005. Seasonal core area ranges were calculated for 61 different fox squirrels with > 30 locations per season; some fox squirrels had ranges calculated during multiple seasons (winter = 32, spring = 13, summer = 13, fall = 17). Fox squirrels overwhelmingly selected for tree canopy at all scales and during all seasons while active and inactive (Figures 2.2-2.4). Fox squirrels showed differential use of the other 3 substrates (pavement, grass, and buildings) based on temporal (seasonal), spatial (point-study area, range-study area, and point range) and behavioral (active and inactive) scales. Fox squirrels were not observed using grass or pavement during periods of inactivity (Figures 2.2, 2.4); however, fox squirrels did select to use buildings within their core areas as a substrate and day time refugia (inactive) during the

winter ($S = 1.96$) and spring ($S = 1.12$) (Figure 2.4). Active fox squirrels avoided buildings in their core areas during the spring ($S = 0.53$) summer ($S = 0.45$) and fall ($S = 0.54$) (Figure 2.4). Fox squirrels showed a clear pattern of avoiding pavement as a substrate (Figures 2.2, 2.4) but did not appear to exclude pavement from their core areas (Figure 2.3). Fox squirrels selected grass in their core areas during activity periods, especially in the spring ($S = 1.83$) (Figure 2.4); however, they disproportionately excluded grass from their core areas during the winter ($S = 0.68$) and summer ($S = 0.73$) (Figure 2.3).

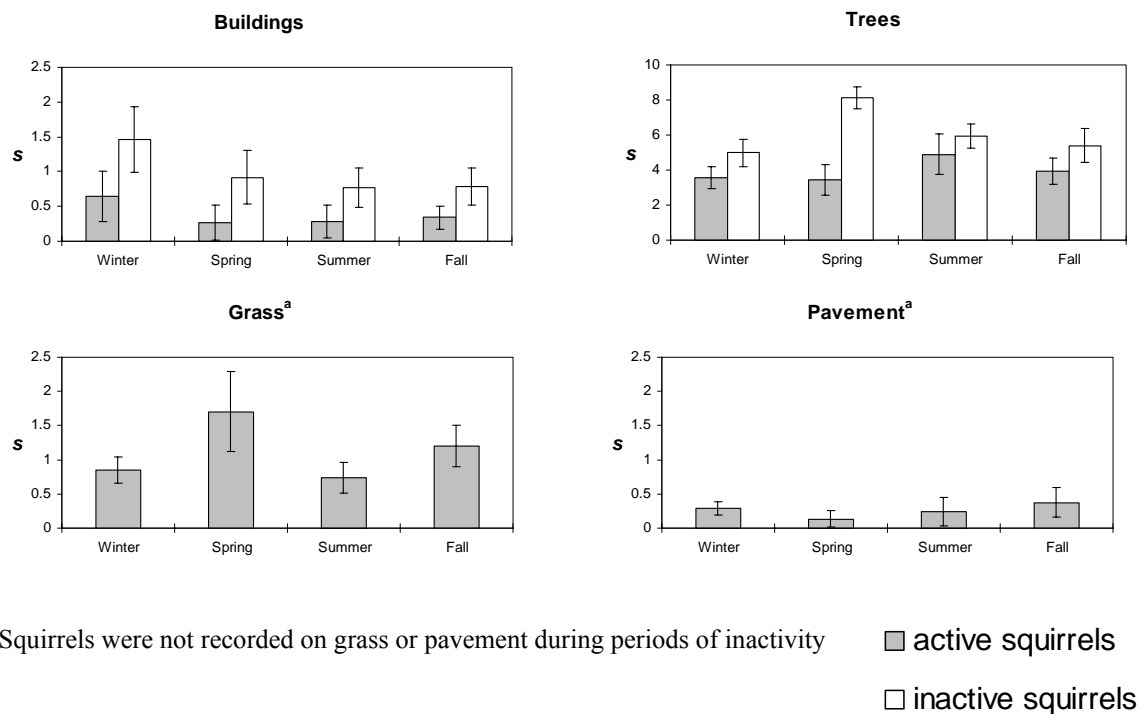


Figure 2.2 Fox squirrels averaged point-study area selection ratios of urban substrates (buildings, tree = tree canopy, pavement = concrete, asphalt, brick, and grass = manipulated grass areas) and 95% CI error bars by season and activity (active and inactive), in College Station, Texas, USA.

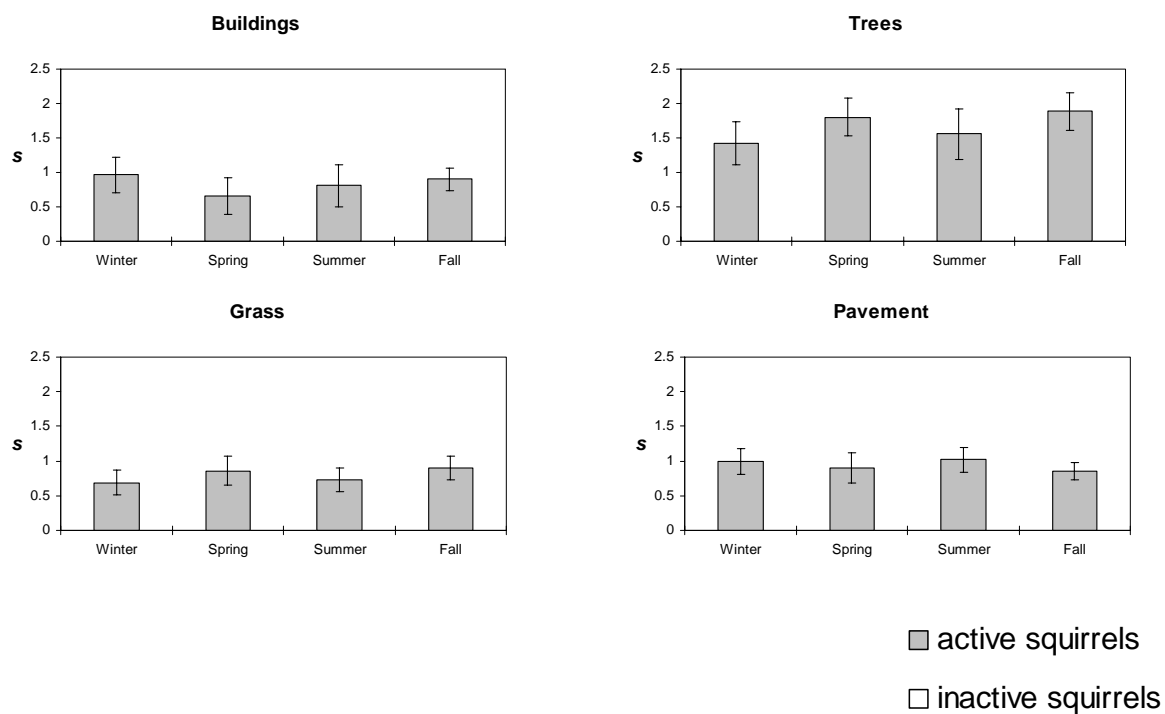


Figure 2.3. Fox squirrels averaged range-study area selection ratios of urban substrates (buildings, tree = tree canopy, pavement = concrete, asphalt, brick, and grass = manipulated grass areas) and 95% CI error bars by season, in College Station, Texas, USA.

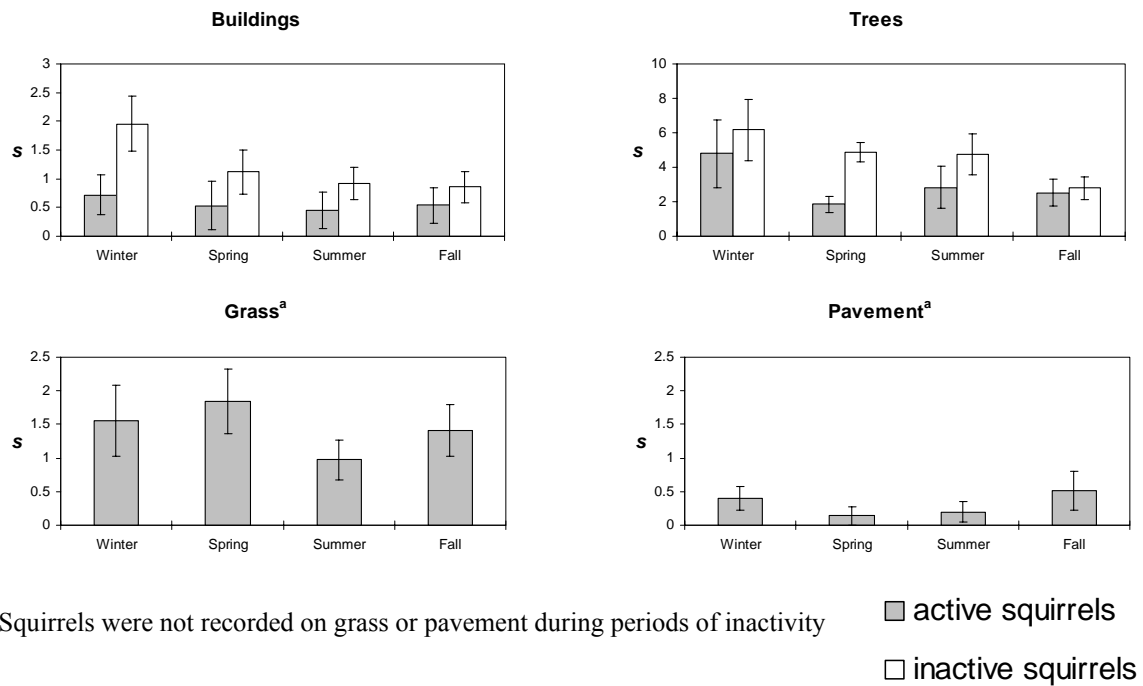


Figure 2.4. Fox squirrels averaged point-range selection ratios of urban substrates (buildings, tree = tree canopy, pavement = concrete, asphalt, brick, and grass = manipulated grass areas) and 95% CI error bars by season and activity (active and inactive), in College Station, Texas, USA.

In my analysis of tree selection, active fox squirrels avoided pines, bald cypress, and arborvitae (Table 2.1). During these periods of activity fox squirrels selected to use live oaks with a greater canopy area (95% CI = 36.6–40.2 m) and DBH (95% CI = 19.1–20.9 cm). During periods of inactivity fox squirrels used live oaks more than expected and bald cypress, Bradford pear, and arborvitae less than expected. When taking refuge (inactivity) fox squirrels selected elms (95% CI = 25.5–31.1 m), Chinese pistachio (95% CI = 30.4–43.4 m), bald cypress (95% CI = 27.7–32.3 m) and live oaks (95% CI = 38.6–41.6 m) with greater canopy than trees of the same species. Likewise, fox squirrels used live oaks (95% CI = 19.7–21.1 cm), post oaks (95% CI = 19.6–22.2 cm), other oaks (95% CI = 12.7–25.4 cm), Chinese pistachio (95% CI = 14.0–22.2 cm), bald cypress (95% CI = 11.7–16.3 cm), and elm (95% CI = 10.3–12.8 cm) with larger DBH during periods of inactivity.

In the initial evaluation of fox squirrel activity on a 1 ha resolution spatial scale, I found the $\Delta AICc$ and w_i values from *a priori* Models 4, 5 and the global model (10) to be the best approximating of the data and used them to generate *a posteriori* models (Table 2.2). Comparing all models, again using $\Delta AICc$ and w_i values, I selected the global model and Model 11 as competing best approximating models (Table 2.2). They had a combined $w_i \geq 0.84$, suggesting there is $\geq 84\%$ probability that one of these 2 models yielded the best explanation of the data. My examination of individual parameters showed that only the parameter estimate and 95% CI of *ntress* contained zero, suggesting that the number of trees was the only variable that was not a relevant predictor of fox squirrel activity (Table 2.3).

Table 2.1. Urban fox squirrel observed versus expected use of tree by species groups during periods of activity and inactivity with 95% CI, and average canopy area (2 dimensional area cover by tree branches and leaves) and DBH measures with 95% CI for trees with active squirrel, inactive squirrels and no squirrels recorded (absent) by trees species group, College Station, Texas, USA.

Species group	squirrels	<i>n</i>	observed frequency		% expected		DBH			canopy area		
			%	95% CI			Mean	95% CI		Mean	95% CI	
Live oak	active	211	8.8	6.78–8.8	7.69	p	20.0	19.1–20.9	b	38.4	36.6–40.2	b
	inactive	319	13	10.57–13.0	10.14		20.4	19.7–21.1	b	40.1	38.6–41.6	b
	absent	1,097					15.8	15.4–16.9		31.3	30.6–32.1	
Post oak	active	34	1.67	0.84–1.67	1.44		20.7	18.6–22.8		33.0	29.2–36.8	
	inactive	58	2.69	1.68–2.69	1.89		20.9	19.6–22.2	b	36.0	33.4–38.6	
	absent	211					18.6	17.8–19.4		32.0	30.3–33.7	
Other oaks	active	17	0.93	0.33–0.93	0.52		12.4	8.0–16.8		31.0	22.3–39.7	
	inactive	12	0.77	0.23–0.77	0.69		19.0	12.7–25.4	b	35.0	23.5–46.6	
	absent	79					8.4	7.5–9.3		22.5	20.5–24.5	
Chinese pistachio	active	10	0.6	0.14–0.60	0.29		10.9	6.9–14.9		27.6	19.7–35.5	
	inactive	9	0.55	0.12–0.55	0.39		18.1	14.0–22.2	b	37.1	30.4–43.4	b
	absent	43					10.0	8.3–1.7		26.2	22.5–29.9	
Pines	active	2	0.18	0–0.18	0.21	a	8.5	7.5–9.5		20.5	17.7–23.3	
	inactive	5	0.35	0.02–0.35	0.28		12.0	8.4–15.6		28.6	20.7–36.5	
	absent	37					10.9	9.5–12.3		24.0	20.7–27.3	
Bald Cypress	active	4	0.29	0–0.29	0.33	a	13.5	11.2–15.8	b	29.0	27.5–30.5	b
	inactive	3	0.24	0–0.24	0.44	a	14.0	11.7–16.3	b	30.0	27.7–32.3	b
	absent	62					6.5	5.5–7.5		15.9	13.2–18.2	

Table 2.1. (Continued)

Species group	squirrels	n	observed frequency		% expected		DBH		canopy area	
			%	95% CI			Mean	95% CI	Mean	95% CI
Arborvitae	active	6	0.4	0.04–0.40	0.47	a	11.3	6.4–16.2	12.0	7.1–16.9
	inactive	7	0.45	0.01–0.45	0.61	a	10.1	4.5–15.7	19.4	8.8–30.0
	absent	82					8.8	7.5–10.1	17.7	15.8–19.6
Bradford Pear	active	20	1.06	0.42–1.06	0.67		8.2	6.9–9.5	21.3	17.6–25.0
	inactive	8	0.5	0.09–0.50	0.88	a	8.1	5.7–10.5	22.0	16.1–27.9
	absent	135					7.0	6.4–7.6	16.7	15.4–18.1
Elms	active	28	1.33	0.61–1.33	1.03		11.4	9.7–13.1	26.2	23.7–28.7
	inactive	33	1.63	0.81–1.63	1.37		11.5	10.3–12.8	28.3	25.5–31.1
	absent	156					9.1	8.3–9.9	23.8	22.2–5.4
Fruit trees	active	9	0.55	0.12–0.55	0.42		6.0	3.9–8.1	15.3	10.4–20.2
	inactive	6	0.45	0.01–0.45	0.55	a	7.3	5.1–9.5	22.0	16.2–27.7
	absent	70					5.9	5.2–6.6	17.1	15.4–18.8

a = avoided, observed value < expected value

b= > trees without squirrels absent)

p = preferred, observed values > expected value

Table 2.2. *A priori* and *a posteriori* models relating squirrel activity (the number of squirrel locations in 1-ha blocks) to urban habitat components in College Station, Texas, USA. The Akaike Information criteria adjust for small sample size (AICc), change in AICc from the smallest AICc value ($\Delta AICc$), Akaike weights (w_i) and the number parameters (K) are displayed for each model.

Model ^a	K	AIC _c	ΔAIC_c	w_i
a priori models				
1 None	2	-18409	67.1	0.000
2 Ntrees + canopy + oaks + large	6	-18458	18.2	0.000
3 Grass + oaks + ntrees	5	-18427	49.7	0.000
4 Pave + grass + large	5	-18464	12.8	0.001
5 Build + large + canopy	5	-18471	5.3	0.039
6 Medium + large	4	-18447	29.5	0.000
7 Large + oaks	4	-18449	27.6	0.000
8 Oaks + grass	4	-18423	53.8	0.000
9 Canopy + oaks	4	-18442	34.7	0.000
10 Ntrees + grass + canopy + build + pave + medium + large + oaks	10	-18475	1.3	0.285
a posteriori models				
11 Large + build + canopy + pave + grass	7	-18477	0.0	0.559
12 Large + build + canopy + pave + oaks	7	-18469	7.1	0.016
13 Large + build + canopy + pave	6	-18469	7.3	0.014
14 Large + build + canopy + grass	6	-18470	6.8	0.018
15 Large + build + canopy + oaks	6	-18471	5.1	0.044
16 Large + build + canopy + oaks + grass	7	-18470	6.5	0.022

^a Variable notation for habitat components of 1-ha blocks: none = intercept only, ntrees = total number of trees, grass = area of grass, canopy = ln (canopy area), build = area of buildings, pave = area of pavement, concrete and asphalt, medium = number Of trees with DBH >14 but <20 cm, large = number of trees with DBH >20 cm, oaks = number of oaks.

Table 2.3. Averaged model parameter estimates and 95%CI relating squirrel activity to urban habitat components.

Urban habitat components		95% CI
Large	0.140	0.081 to 0.199
Build	-5.949	-11.718 to -0.181
Canopy	0.334	0.147 to 0.522
Grass	-2.866	-5.924 to -.0245
Medium	-7.645	-12.621 to -2.689
Pave	-8.006	-13.267 to -2.745
Ntress	0.004	-0.027 to 0.035
Oaks	-0.050	-0.097 to -0.003

^a Variable notation for habitat components of 1-ha blocks: large = number of trees with DBH >20 cm, build = area of buildings, canopy = ln (canopy area), grass = area of grass, ntrees = total number of trees, medium = number of trees with DBH >14 but <20cm, pave = area of pavement, concrete and asphalt, oaks = number of oaks.

Discussion

Fox squirrels in the study preferred live oaks and trees with a greater DBH and canopy cover. They also selected tree canopy as a preferred substrate during active and inactive periods, and concentrated movements in areas with proportionally greater tree canopy. These findings are congruent with research on fox squirrels in forested areas showing that large trees and hardwoods are preferred for daytime refugia, presumably because of the shelter and protection from predators they provide (Conner and Godbois 2003).

Our study and findings differed from studies in non-urban areas by examining fox squirrels use of exotic and introduced trees commonly found in urban environments.

A micro-analysis of tree selection indicated fox squirrels avoided introduced pines and other conifers (Table 2.1), suggesting that urban fox squirrels were not using pine seeds and other conifer fruit as food sources, as observed in other studies (Baker 1944, Kantola and Humphrey 1990, Steele and Koprowski 2001). For daytime refuge trees, fox squirrels also avoided pines, along with bald cypress, arborvitae, Bradford pear, and fruit trees (Table 2.1), all of which were prevalent on the study site and common in urban areas in the southeastern United States (Gilman 1997).

Our examination of fox squirrel use of urban substrate on various scales also illuminated the fox squirrels' ability to use an environment that is uninhabitable to many other mammal species (Adams et al. 2006). In the study, fox squirrels selected buildings within their ranges (point-range scale) (Figure 2.3) during the winter and spring, that likely provided safe, warm refugia. During the study, I noted female fox squirrels used buildings in the late winter and early spring to raise their young. The use of buildings might be more pronounced in northern urban areas where the numbers of nest cavities are a limiting factor for many fox squirrel populations (Nixon et al. 1984, Kantola and Humphrey 1990), and could provide a warm refuge from colder temperatures.

Much of the urban environment consists of concrete, pavement, and asphalt (Adams 1994, Adams et al. 2006), which fox squirrels clearly avoided on both the point-study area and point-range scales. Nonetheless, range-study area analysis showed that fox squirrels proportionally included pavement in their core-area ranges (Figure 2.3). This suggests that although fox squirrels were not spending time on pavement, they did not let this seemingly biologically useless substrate limit their movements and areas of

activity. The ability to tolerate pavement in core-area movements and to use buildings makes vast areas of the urban environment available for fox squirrels to exploit.

Considering that pavement and buildings typically can comprise up to 80% of the inner-city environment (Adams et al. 2006) and that squirrel are not restricted to parks, forest fragments, and green areas may help explain their success in urban environments. This ability to adapt to altered environments seems to correspond with their high tolerance for disturbed areas (Salisbury et al. 2004).

Fox squirrels spend considerably more time on the ground than other tree squirrels (Whitaker and Hamilton 1998) and appeared during certain times of the year to use open grassy areas common to many urban areas. Fox squirrels appeared to select or avoid the manicured grassy areas common to urban areas depending on the season. Fox squirrels selected grassy areas within the study area and their core areas during the fall and spring and within their core areas during the winter (Figures 2.2, 2.4). These are times when fox squirrels are most active, burying and retrieving their caches (Baker 1944, Whitaker and Hamilton 1998). Conversely, fox squirrels established core areas that appeared to avoid grass during the summer and winter (Figure 2.3). One possible explanation for these movements is that the squirrels reduced their time in risky environments (open grassy areas) (Lima and Dill 1990) when they were not using them for food storage and recovery.

Results from my analysis of fox squirrel activity models suggest that not only large trees, but multiple features of the urban environment including: the number of buildings, pavement, tree canopy cover, the number of oaks and the number of medium

size trees (>14 cm and ≤ 20 cm DBH) were all important factors in determining fox squirrel activity. Interestingly, the number of trees present was not a relevant predictor of squirrel activity, in addition to the features previously listed. My data suggests that tree size, tree species and canopy cover were more important predictors than tree numbers alone. My effort to simplify and explain fox squirrel activity with a few variables failed, since fox squirrel activity appears to be influenced by numerous features (buildings, pavement, canopy, tree composition) of the urban landscape.

In conclusion, my study suggests that urban fox squirrels have been able, through the process of synurbanization, to adapt to urban areas. They made the most of the large mast-bearing trees that mimicked the habitats that they prefer in non-urban areas, while managing to use, tolerate, or avoid the numerous non-native and man-made features of the urban environment.

Management Implications

Urban landscapes with large trees (Flyger 1974, Adams 1994), buildings, and manicured grass may provide an excellent habitat for fox squirrels. This increases the possibility of fox squirrel damage in some urban areas (Flyger 1974). Nonetheless, planners and landscapers who want to control fox squirrel populations through habitat manipulation (McComb 1984) may have several options. My data suggests that removal or reduction of oaks and other large trees and the reduction of canopy may be one way to address the problem. Trees that have been removed may be replaced with pines, bald cypress, arborvitae, Bradford pear, and fruit trees, which urban fox squirrels appeared to

avoid. Additionally, my data indicates that restricting their access to buildings may control fox squirrel populations in urban areas. Alternatively, to bolster fox squirrel populations in urban areas, large mast bearing trees such as oaks should be planted and canopy cover increased, and sufficient grassy areas for the caching of mast should be increased. In addition, those trying to increase fox squirrel populations without inviting squirrels into buildings might want to consider the use of nest boxes (Nixon et al. 1984).

CHAPTER III

SURVIVAL AND MORTALITY

Synopsis

Mammalian populations that have adapted to urban areas have shown higher rates of survival compared with rural populations. I used fox squirrels, (*Sciurus niger*) to examine differences in survival between urban and rural populations of mammals. My data suggested that the rates of survival differed between urban and rural fox squirrel populations. During the same time period, fox squirrels on the urban site appeared to have reduced mortalities relative to the rural site. My data suggest that sex and season may be bigger factors in influencing survival of the urban squirrels. I also found that the cause of mortalities differed significantly between the urban and rural squirrels, with >60% of mortalities on the rural site caused by predation. In contrast, less than 5% of the mortalities on the urban site were caused by predation and >60% of urban fox squirrel mortalities were caused by motor vehicle collisions.

Introduction

In North America, as in the rest of the world, there is a continued trend of increased urbanization (Adams et al. 2005). Wildlife habitats are continually being altered from forest, prairie, swamp and desert into areas dominated by buildings, pavement, and exotic plants. These alterations of the landscape have inevitably impacted wildlife populations in and around urbanized areas (Adams et al. 2006). Many

wildlife populations have been unable to cope with urban landscapes while others have adjusted. The process by which some wildlife populations adjust to urban environments is synurbanization (Adams et al. 2005). By understanding synurbanization, one can better predict, accommodate, and manage wildlife populations as they respond to increased urbanization.

Mammalian populations that have adapted to urban areas have shown higher rates of survival compared with rural populations, especially in the winter (Gliwicz et al. 1994, Adams et al. 2005). Differences in survival rates may be due to a reduction of predators, along with favorable climatic and food conditions found in urban areas (Adams et al. 2005). If survival rates of urban wildlife populations, or even segments of urban populations (by age or sex) are consistently higher or even different from rural populations, this could lead to fundamentally different population structures in urban areas. As a result, urban wildlife populations could display differing sex ratios, densities, and age structures in comparison to populations found in rural areas.

I used fox squirrels (*Sciurus niger*), a common tree squirrel found throughout rural and urban areas in mid-western and southeastern United States (Adams 1994, Flyger 1974), to examine differences in survival between urban and rural populations of mammals. Previous studies in rural areas have shown no detectable variation in fox squirrel survival rates when the sexes were compared or when populations were compared during different seasons (Koprowski 1994, Steele and Koprowski 2001, Conner 2004). However, it appears that squirrel survival is influenced by extreme changes in food availability (Steele and Koprowski 2001). No research has been

performed on the survival rates or causes of mortality in an urban population of fox squirrels to determine whether they show similar patterns to those seen in rural populations. I tested the hypotheses that survival and causes of mortality differ between a population of mammals found in an urban area and an adjacent population of the same species found in a rural environment. If survival and mortality differed in urban and rural areas, I wanted to further investigate the assertion that differences would be pronounced by season. Additionally, I hypothesized that the biological and behavioral differences of males and females would result in different rates of survival and differing causes of mortality according to sex.

To test these hypotheses and to further explore the affects of synurbanization on survival, I monitored mortality and survival of 2 populations of fox squirrels. One population was located in an urban setting while the other was located in a rural setting. The specific corresponding objectives to my study were to: (1) compare survival between urban and rural areas, (2) determine the effects of sex and season on survival of both the urban and rural populations and (3) identify and compare the causes of mortality in both urban and rural areas.

Methods

Study Areas

Research on an urban population of squirrels was conducted on 140 ha of the main campus of Texas A&M University, College Station, Texas, USA. Over 45,000 students attended the university during the study and there was a nearly constant flow of

pedestrians and vehicles on the campus. The urban site was comprised of a dense cluster of buildings, parking lots, and streets. Extending out from this aggregation of buildings was an area of buildings with lawns and even sparsely forested openings with no understory, portions of which are reminiscent of many parks and cemeteries found in suburban areas (Adams 1994). Some of the dominant trees species found on the urban study site were live oak (*Quercus fusiformis* and *Q. virginiana*), post oak (*Q. stellata*), Bradford pear (*Pryus calleryana*), arborvitae (*Thuja* spp.), and elm (*Ulmus* spp). Conversely, the study site for a rural population of squirrels was on a private ranch 18-km from the main Texas A&M University campus. The area was surrounded by other ranches and bordered by the Navasota River. The study site was approximately 240 ha of undisturbed bottomland hardwood forest and meadows that had little to no human activity. Fox squirrels had not been hunted or fed on this site for over 20 years. Some of the dominant trees species in the area included post oak (*Q. stellata*), water oak (*Q. nigra*), pecans (*Carya* spp.), and elms.

Trapping

In an effort to maintain a continuous sample of 20 squirrels (10 male, 10 female) on each study site equipped with functioning radio-telemetry collars, I trapped squirrels periodically from August 2003 through June 2005 on the urban study site and from May 2004 through July 2005 on the rural study site. To trap squirrels, I strapped >65 Tomahawk wire-cage traps (No. 103, Tomahawk Live Trap Company, Tomahawk, Wisconsin, USA) to the limbs of trees (Korschgen 1981, Adams 1984) on each study

sites. Traps were pre-baited with sunflower seeds and pecans 2–3 days prior to trapping to increase trapping success. Once squirrel were captured they were sexed, aged (Dimmick and Pelton 1996), and weighed. Each squirrel was ear-tagged (Monel 1005-3, National Band and Tag Company, Newport, Kentucky, USA), given a passive integrated transponder (PIT tag, Biomark, Boise, Idaho, USA) and, prior to release, (Korschgen 1981, Samuel and Fuller 1996) adult squirrels with potential reproductive capacities (>7 months old) (McCloskey and Vohs 1971) were fitted with a collar and a battery-powered mortality-sensitive radio transmitters (150–152 MHz, 12 g, model M170 Advanced Telemetry Systems, Isanti, Minnesota, USA or 10g, model MP-2 AVM Instrument Company, Colfax, California, USA). All capturing and handling of fox squirrels was performed in a humane manner under the guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998). In addition, the project was approved by the Texas Parks and Wildlife (Scientific Permit SPR-1101-181) and the Animal Care and Use Committee and Texas A&M University (2001-278T).

Radio Telemetry

I tracked radio-collared squirrels on the urban site for the 24-month period (21 September 2003 through 21 August 2005) and on the rural site for the 18-month period (21 June 2004 through 21 December 2005). I monitored squirrels locations 2–3 times/week at random intervals (16-hour period divided into 8 equal 2-hour segments; one 2-hour segment was randomly selected and during that time all squirrels were located). After receiving a mortality signal, I immediately located the collar. The collar,

squirrel remains, and evidence in the surrounding area were examined to determine cause of death (Adrian 1996). Mortalities were placed into 1 of 5 categories: mammalian predation, avian predation, vehicular collision, other (drowning, poisoning), and unknown.

Data Analysis

I converted radio-telemetry data into encounter histories and used Program MARK to generate monthly known-fate-survival estimates. Encounter histories consisted of the number of squirrels available at the beginning of each month and the number of mortalities occurring during each month grouped by site and sex. I censored animals during the last month that their radios failed or disappeared (Pollock et al. 1989).

I used an information-theoretic approach (Burnham and Anderson 1998) to evaluate monthly survival and survival by site, sex, season and year. I used Program MARK to evaluate 3 sets of *a priori* models. For the urban study site (*urban*), I generated 8 models to evaluate the influence of sex and season. I defined seasons (*season*) as 4, 3-month periods resembling commonly defined calendar seasons with fall beginning on 21 September and I defined 2-yearly periods (*year*) beginning on 21 September 2003 and 21 September 2004. For the rural site (*rural*), I evaluated 5 models comparing survival by sex, season of the year (*season*), and each of the 6 seasons the squirrels were tracked (*season year*). To compare survival between the study sites (*combined*), I evaluated seasonal and site specific models, pooling the data by sex. I

compared survival between sites for the 12 months the sites simultaneously had >19 individual radio-tagged squirrels (21 July 2004 through 20 July 2004). All 3 sets of models contained a constant model representing no fluctuation in the survival rates. Models were evaluated using ΔAICc , the relative difference to the smallest AICc (Akaike's Information Criterion corrected for small sample size), and Akaike weights (w_i) (Burnham and Anderson 1998). I considered models ≤ 2 AICc units to compete with the best model, models $> 2 \leq 4$ AICc units from the best model were considered plausible, while models > 4 AICc units were disregarded as an unlikely representation of the data (Burnham and Anderson 1998). I calculated model-averaged 95% confidence intervals for monthly survival rates with a logit transformation (Burnham et al. 1987) and presented parameter estimates of all models ≤ 4 AICc of the best model and a lower AICc value than the constant model.

I examined the differences in 3 categories of cause-specific mortalities (avian and mammalian predation, vehicular collision, and unknown and other were pooled to increase sample size) between sites, between sex on both sites, and among season on the urban site using contingency tables and a Pearson χ^2 test (Simonoff 2003). I calculated observed values as the number of mortalities occurring for each category by sex, season, or site. I determined expected values by multiplying the total number of mortalities by the proportional amount of months that squirrels were available for season, sex, or site. Due to only 1 recorded occurrence of predation on the urban site, predation was not included in analysis of the urban study.

Results

I captured, radio-collared and tracked 128 fox squirrels, 50 (30 male, 20 female) on the rural site and 78 fox squirrels on the urban site (41 male, 37 female), for an average of 5.4 months per squirrel. I compared rates of survival between the rural and urban site and found the best approximating model for the *combined* model set to be a model that separated the data by site (Table 3.1). The site model had an Akaike weights >2 times larger than a constant model, suggesting it was twice as likely to reflect the data. Survival on the rural study site appeared to be lower on the rural study site during this 12-month interval (Table 3.2). Models including year, year and sex, season, and a constant value were all plausible models (≤ 4 AICc units from the best model) for explaining variation on the urban study site. Nonetheless, models with year and year and sex could be considered as competing best approximating models with a combined Akaike weight >70 (Table 3.1). On the urban study site, survival appeared to be lower during year 1 (2004) and higher during year 2 (2005), while survival for males appeared lower than females during year 1 and higher than females during year 2 (Table 3.2). Models including sex and season were plausible models for survival on the rural site; however, the model with a constant survival rate had the lowest AICc value and an Akaike weight more than double the next closest model (Table 3.1).

Table 3.1. A comparison of 3 sets of *a priori* models used to analyze the influence of season, year, sex and site on the survival of fox squirrels from September 2003 through September 2005 in College Station, Texas, USA.

Model sets ^a	Model ^b	K ^c	AICc ^d	Δ AICc ^e	w _i ^f
Combined	{site }	2	140.54	0	0.690
	{constant}	1	142.48	1.94	0.261
	{season}	4	145.85	5.31	0.049
Urban	{year}	2	193.14	0	0.450
	{year sex}	4	194.27	1.13	0.256
	{season}	4	196.19	3.05	0.098
	{constant}	1	196.91	3.77	0.068
	{season year}	8	197.15	4.01	0.061
	{season year sex}	12	198.03	4.89	0.039
	{sex}	2	198.93	5.79	0.025
	{season sex}	8	203.40	10.26	0.003
Rural	{constant}	1	118.33	0	0.546
	{sex}	2	119.94	1.61	0.244
	{season sex}	7	121.42	3.09	0.116
	{season}	4	123.14	4.81	0.049
	{season year}	6	123.35	5.02	0.044

^a Model sets: combined = survival on urban and rural sites from 21 July 2004 through 20 July 2004, urban = survival on urban site 21 September 2003 through 21 August 2005, rural = survival on rural site 21 June 2004 through 21 December 2005.

^b variables: constant= constant survival, sex = male and female, year = (year 1= 21 September 2003 through 20 September 2004, and year 2 = 21 September 2004 through 20 September 2005), season = (winter = 21 December through 20 March, spring = 21 March through 20 June, summer = 21 June through 20 September, fall = 21 September through 20 December),

* season year in the rural model set considers each of the 6 seasons form 21 June 2004 through 21 December 2005 independently

^c Number of parameters in each model

^d Akaike's Information Criterion adjusted for small sample size

^e Difference between AICc of the model and the best model

^f Akaike weight

Table 3.2. Monthly averaged survival (\hat{S}) estimates, SE, and 95% CI for parameters of best approximating models of fox squirrel survival from September 2003 through September 2005 in College Station, Texas, USA. Best approximating models were ≤ 4 AICc (Akaike's Information Criterion adjusted for small sample size) units of lowest AICc valued model with a lower AICc than a constant survival model.

Models sets ^a	Parameter ^b	\hat{S}	SE	95% CI	
				Lower	Upper
Combined	Urban	0.976	0.011	0.944	0.990
	Rural	0.936	0.018	0.891	0.963
	Constant	0.957	0.010	0.932	0.973
Urban	Year 1	0.913	0.019	0.869	0.943
	Year 2	0.968	0.013	0.931	0.986
	Male year 1	0.904	0.025	0.842	0.944
	Female year 1	0.926	0.027	0.852	0.964
	Male year 2	0.989	0.011	0.925	0.998
	Female year 2	0.949	0.022	0.884	0.979
	Fall	0.941	0.022	0.882	0.972
	Winter	0.974	0.015	0.922	0.991
	Spring	0.887	0.032	0.807	0.936
	Summer	0.944	0.024	0.872	0.976
	Constant	0.938	0.012	0.910	0.957
Rural	Constant	0.945	0.014	0.911	0.967

^a Model sets: combined = survival on urban and rural sites from 21 July 2004 through 20 July 2004, urban = survival on urban site 21 September 2003 through 21 August 2005, rural = survival on rural site 21 June 2004 through 21 December 2005.

^b Parameters: constant = constant survival, year 1 = 21 September 2003 through 20 September 2004, and year 2 = 21 September 2004 through 20 September 2005, winter = 21 December through 20 March, spring = 21 March through 20 June, summer = 21 June through 20 September, fall = 21 September through 20 December.

Table 3.3. Cause specific mortalities of fox squirrels from September 2003 through September 2005 on an urban and rural site in College Station, Texas, USA.

Site	Sex	<i>n</i>	Months at risk	Predation		Vehicle collision	Unknown	Other ^a	Total
				Avian	Mammal				
Rural	Male	30	168	2	3	0	3	0	8
	Female	20	111	1	3	0	2	0	6
Urban	Male	41	226	0	0	9	2	3	14
	Female	37	193	1	0	6	3	2	12

^aother included drowning and poisoning

I recorded 40 mortalities on the 2 sites (Table 3.3). Fifteen of the 26 mortalities on the urban site were caused by vehicular collisions and only 1 predation event was recorded. Additionally, on the urban site, I found 3 squirrels drowned in opened drainage pipes and 2 squirrels were poisoned; all 5 were placed in the other category to represent anthropogenic causes of mortality. On the rural site, I classified 9 of the 14 mortalities as being caused by predation. The other 5 mortalities on the rural site were listed as unknown because there were insufficient remains to determine the cause of death. Causes of mortality differed between the study sites ($\chi^2_5 = 22.26, P < 0.001$) but I did not detect a difference by sex on the urban ($\chi^2_3 = 0.28, P = 0.961$) or rural site ($\chi^2_3 = 0.07, P = 0.994$) or by season on the urban site ($\chi^2_7 = 5.57, P = 0.594$).

Discussion

In accordance with synurbanization theory, my data suggested that rates of survival differed between urban and rural fox squirrel populations. During the same time period, fox squirrels on the urban site appeared to have increased rates of survival relative to the rural site. I could not disprove my hypothesis that causative agents of mortalities differed between urban and rural areas, and found that they differed significantly between the sites. Additionally, my data did not refute the belief that higher survival in urban areas are in part due to the reduced risk of predation (Adams et al. 2005). At least 60% of the mortalities on the rural site were caused by predation, while less than 5% of the mortalities on the urban site were caused by predation.

Although, I found that the causes of mortality differed considerably between the sites, I did not find the cause of mortality to differ by sex as I had hypothesized. Nonetheless, my data suggests that sex and season may both be greater factors in influencing survival on the urban site than on the rural site. Season was considered a plausible model of squirrel survival on the urban site, and in accord with other research on small mammals in urban settings where survival appeared to decrease during the winter (Table 3.2) (Gliwicz et al. 1994, Adams et al. 2006). Sex was a variable in a competing best approximating model, but the relationship between sex and survival was difficult to discern because male survival high during the first year and considerably decreased during the second (Table 3.2).

The 2 best approximating models of survival on the urban site included the variable year, with a combined Akaike weight of >75 . During the first year of the study the fox squirrel population monthly survival was 0.913 but increased to 0.968 during the second year (Table 3.2). The best approximating model for the rural population over the 18-month period was a model of constant mortality (0.945), consistent with research indicating that rural squirrel populations have a relatively constant rate of survival (Conner 2004). Comparing yearly results on the urban site with the 18-month period on the rural site suggests that it might not be accurate to portray urban wildlife populations with reduced predation as having higher rates of survival. Instead, it may be more accurate to suggest that differential agents of mortality in urban areas can simply be reflected in different rates or patterns of survival from rural populations.

One explanation of the fluctuating survival rates on the urban site may be that the causative agents have a relationship with population density. Over 60% of the mortalities on the urban site were caused by motor vehicle collisions, a common cause of death for many urban wildlife species (Adams et al. 2006). It seems logical to suggest that as the number of squirrels in an area increase so will the number of squirrel road crossings and, in turn, squirrel mortalities. A similar pattern has been shown in some urban deer populations (Lopez et al. 2003). A possible explanation of urban squirrel susceptibility to vehicle collisions may be deducted from the way they use the urban environment. A recent study indicated that urban squirrels do not avoid concrete in their core area movements (Chapter II). Consequently, unlike some other urban mammals (Gehrt 2005, McCleery et al. 2006b) roads do not appear to create a barrier to squirrel movements.

What appears clear from my study is a need to understand urban wildlife and their population dynamics separately from their rural counterparts. The differences between rural and urban populations highlight the need to further develop a body of literature on synurbanization in hopes of understanding, predicting, and mitigating the effects of urbanization on wildlife resources.

CHAPTER IV

ANTI-PREDATOR BEHAVIORS ACROSS THE URBAN-RURAL GRADIENT

Synopsis

The continuous predator stimuli created directly and indirectly by humans in the urban environment may alter animals' anti-predator behaviors. I expect these alterations in behavior to occur across the urban-rural gradient as the density and presence of humans change. I hypothesize that anti-predator behaviors in response to humans would decrease from rural to urban settings and that the mechanism for this change would be habituation. Additionally, I hypothesize that populations habituated to humans would show a reduced response to predator stimuli in environments of low predation risk. To test these hypotheses, I observed 3 populations of squirrels (urban, suburban and rural) for responses to human approaches, red-tailed hawk vocalizations (*Buteo jamaicensis*) and coyote (*Canis latrans*) vocalizations. My data supported the hypothesis of decreased anti-predator behaviors, indicating that flight initiation distances ($X^2 = 26.33$, $df = 2$, $P < 0.001$) and amount of time dedicated to anti-predator behavior ($X^2 = 10.94$, $df = 2$, $P = 0.004$) were different among sites. Manhaloblis distances of all anti-predator behaviors were consistent with the urban-rural gradient. In support of my hypothesis of habituation, naive juvenile squirrels showed increased flight initiation distances ($X^2 = 35.89$, $df = 1$, $P < 0.001$) and time dedicated to anti-predator behaviors ($X^2 = 9.46$, $df = 1$, $P = 0.002$) relative to adult squirrels in the same urban environment in response to human approaches. In support of my final hypothesis, the amount of time dedicated to

anti-predator behaviors differed among all 3 sites in response to both coyote ($X^2 = 9.83$, $df = 2$, $P = 0.007$) and hawk ($X^2 = 6.50$, $df = 2$, $P = 0.035$) vocalizations. Responses to both vocalizations on rural sites (coyote = 45%, hawk = 55%) averaged at least twice that found on the urban sites (coyote = 11%, hawk = 20%), in areas which were shown to have a significantly reduced risk of fox squirrel predation. This is the first documented case of a possible transfer of habituation demonstrated under field conditions.

Introduction

Urbanization of the planet's landscapes has created new environments that are evolutionarily novel to wildlife species (Adams et al. 2005). Many wildlife species have been unable to utilize these new environments, while others have through the alteration of their population dynamics, physiology, behavior, movements, and habitat selection (VanDruff et al. 1996, Adams et al. 2005). Most studies of the impacts of urban environments on wildlife have focused on population dynamics and habitat use (Adams et al. 2005) with little attention being given to behavioral changes of wildlife in urban areas (Bowers and Breland 1996). Understanding the behavioral changes of wildlife in urban settings can help in the management of urban wildlife, and to identify the reasons behind demographic population level changes and physiological changes that are common in those populations (Bowers and Breland 1996, Metcalf et al. 2000).

Studies of urban wildlife should account for the reality that urban landscapes are diverse (Matson 1990). Fortunately, regardless of their complexity, urban landscapes

usually follow a consistent pattern of heavy human alteration and human presence in a city center, that is gradually reduced as the city extends outward to more natural or rural areas (Adams 1994). This landscape transition is commonly referred to as the urban-rural gradient (Matson 1990). Instead of simply looking at anthropogenic effects on wildlife at the extremes of the gradient (in city centers and rural areas), examination of the gradient can yield a more complete picture of the extent to which urbanization impacts wildlife populations (Matson 1990, Bowers and Breland 1996)

Across the urban-rural gradient (and in all landscapes) animals make behavioral choices to balance the risks of predation with the risks of starvation (Brown 1999, Brown et al. 1999, Olsson et al. 2002). There are at least 2 characteristics that increase with the degree of urbanization that should theoretically affect the behavioral choices made by wildlife when balancing predation risks with foraging. First, as urbanization increases toward the city center so does the presence of humans, who are directly and indirectly responsible for almost constant predator stimuli for the animals in these environments. These disturbances even without the risk of predation may negatively alter an animal's behavior by increasing vigilance behaviors (Berger et al. 1983, Frid and Dill 2002). Animals use vigilance behaviors such as scanning and listening for predators and other anti-predator behaviors such as running, remaining still, alarm calls or threatening gestures to avoid predation (Brown 1999, Alcock 2001). Anti-predator behaviors and vigilance may reduce an animal's risk of predation (Lima and Dill 1990); however, when the risk of predation is not real (human disturbance) these behaviors can have a negative effect. By limiting the amount of time available for foraging, vigilance

and anti-predator behaviors can reduce an animal's energy intake, body condition, and reproductive success (Lima and Dill 1990, Brown 1999).

One well known way that researchers have attempted to measure the impact of human disturbances on wildlife populations is to measure the distance to which humans can approach before an animal flees; this measure is commonly called the flight initiation distance (Lima and Dill 1990). In urban areas vertebrate species have generally (Knight et al. 1987, Labra and Leonard 1999, Magle et al. 2005) shown decreased flight initiation distances relative to their rural counterparts, indicating that they have a reduced wariness to humans. In spite of the reduced wariness, studies have suggested that the vigilance of urban species is still higher than their rural counterparts (Ward and Low 1997, Randler 2003) but no studies have quantified the differences in behaviors of animals' response to humans. Here I attempted to determine whether animals in urban environments not only reduce their flight initiation distances but, also, alter the amount and types of vigilance and anti-predator behaviors in response to humans.

It has been hypothesized that animals in urban areas that are continually exposed to human stimuli reduce their anti-predator responses and their vigilance behavior through a process of habituation (Knight et al. 1987, Metcalf et al. 2000, Reimers and Sigurd 2001, Magle et al. 2005). In other words, animals have developed a decreased responsiveness to the repeated exposure of the human stimulus (McFarland 1993) so that they can better cope with the urban environment. Nonetheless, Frid and Dill (2002) claim that habituation to non-lethal human disturbance is usually only partial (Burger

and Gochfeld 1981, Burger and Gochfeld 1990) and in some cases animals can even show a stronger anti-predator response to non-lethal disturbances after frequent exposure to them (Dill 1974, Magle et al. 2005). Still, without some mechanisms to reduce behavioral responses to humans, animals would be unlikely to utilize urban environments. I contend that vertebrate species that have been successful in utilizing urban habitats will show a reduction in anti-predator responses and vigilance behaviors, and that the mechanism for the reduction of their anti-predator behaviors is habituation.

The second factor of urban environments that should affect animals' behavioral choices is a reduction in the risk of predation along the urban-rural gradient due to the elimination and avoidance of predators from most urbanized areas (Blumstein 2002, Lopez et al. 2003, Adams et al. 2005). Coss (1999) hypothesized that a reduced or eliminated threat of predation (Anchor et al. 2002, Lopez et al. 2003) in areas may reduce the need for anti-predator behaviors. Moreover, Olsson et al. (2002) presented a model of predation risk that predicts populations with extremely low predation risk, like those found in urban areas, should be free to reduce their use of anti-predator behaviors (Brown 1999, Frid and Dill 2002, Fritz et al. 2002). Nonetheless, this hypothesis and model do not explain what mechanism might cause animals foraging in areas of minimal predation to reduce their vigilance and anti-predator behaviors. I believe that one mechanism that might allow animals to reduce their vigilance especially in urban areas is the transfer of habituation (Hinde 1954).

A potential artifact of habituation to human stimuli may be a reduced response toward other stimuli (Hinde 1954). This transfer of habituation has been shown in

laboratory settings but is not known to occur in the wild (Curio 1993); however, researchers have not investigated the different circumstances under which the transfer of habituation may occur (Curio 1993). I believe 1 reason that field studies have failed is that the field setting contains a high risk of predation (Labra and Leonard 1999). Although, the animals' were habituated to 1-predator stimuli (humans), other stimuli were eliciting useful anti-predator responses to potential predators. So, when presented with new stimuli the animal reacted as if it were responding to a predator

I believe that in a lab setting or an urban setting with little or no real risk of predation to many species, animals should transfer their habituated response to humans toward other stimuli. As the risk of predation increases along the urban rural-gradient, I would expect to see a reduction in the transfer of habituation to predator stimuli.

To investigate the differences in anti-predator behaviors, habituation, and the transfer of habituation along the urban-rural gradient, I used fox squirrels (*Sciurus niger*). I chose squirrels because they are common and observable in urban and rural environments (Conover 1997, Adams et al. 2006) and have been commonly used in models to investigate hypotheses of vigilance behaviors (Lima and Valone 1986, Newman et al. 1988, Bowers and Breland 1996).

The purpose of my research was to understand the relationships between the urban environment and the behavior of wildlife. I focused inquiries on the mechanisms and influences that affect animals' anti-predator behavior along the urban-rural gradient. I specifically used fox squirrels to test the following 3 hypotheses:

- H1: Flight initiation distances will decrease, the amount of anti-predator behaviors will decrease and the types of anti-predator behaviors will change in response to human approach as the prevalence of humans increases along the rural-urban gradient.
- H2: Reduction of flight initiation distances and anti-predator behaviors along the urban-rural gradient is due to habituation.
- H3: Populations habituated to humans will show a reduced response to predator stimuli in environments of low predation risk.

Methods

Study Areas

I conducted research on 3 sites chosen to represent urban, suburban and rural areas on an urban-rural gradient. The center or urban area of the gradient was represented by 140 ha of the main campus of Texas A&M University in College Station, Texas, USA. Over 45,000 students attended the university during the study and there was a nearly constant flow of pedestrians and vehicles on the campus. The site was comprised of a dense nucleus of buildings, parking lots and streets. Extending out from this nucleus was an area of courtyards like configurations of buildings. Some of the dominant trees species found on the study site were: live oak (*Quercus fusiformis* and *Q. virginiana*), post oak (*Q. stellata*), Bradford pear (*Pryus calleryana*), arborvitae (*Thuja* spp.), and elm (*Ulmus* spp).

To represent the rural end of the urban-rural gradient, I conducted squirrel behavioral observations on a private ranch 18-km from the urban site. The ranch was surrounded by other ranches and bordered by the Navasota River. The portion of the ranch used for research was approximately 240 ha of undisturbed bottomland hardwood forest and meadows that had little to no human activity on it. Squirrels had not been hunted or fed on this site for at least 30 years. Some of the dominant trees species on the site included post oak, water oak (*Q. nigra*), pecans (*Carya* spp.), and elms.

The suburban study site was chosen to represent the middle of the urban-rural gradient. The study site was comprised of 15 suburban parks (Central Park, Oaks Park, Bee-Creek Park, Anderson Park, Brison Park, Hensel Park, Brothers Pond Park, Luther Jones Park, Thomas Park, Henderson Park, Williamson Park, Sue Haswell Park, Tanglewood Park, Sadie Thomas Park and the Bryan Regional Athletic Complex) ranging in size from 10–112 ha. These parks were located on the periphery (5–10 km from the urban site) of the city of College Station, Texas, USA and had a variety of landscapes, but were mostly dominated by oaks with open under stories and grass fields. These parks varied in their rates of human visitation (averaging 32 visitors daily), but all the parks had considerably less human activity than the urban site and considerably more human activity than the rural-study site.

Independent Observations

The urban site was divided into 14 blocks (10 ha), the rural site was divided into 12 (20 ha) blocks, and each of the 15 parks was considered an independent unit (a

block). Each park was separated from the nearest park by >2 km. Blocks were created to ensure independent observation of squirrels and so that no squirrel was sampled twice. Although, squirrel ranges vary and squirrels are not known for territoriality (Steele and Koprowski 2001), telemetry data has shown squirrel ranges to be <10 ha in urban areas (unpublished data, R. A. McCleery, Texas A&M University) and studies of fox squirrels in rural areas of Texas have shown ranges of <20 ha (Geeslin 1970).

Predation Risk

A concurrent study of squirrel predation on the urban and rural sites showed that predation was the most significant source of squirrel mortality on the rural site, but was negligible on the urban site (Chapter III). Predation by either mammals or raptors accounted for $>65\%$ of the mortalities in a radio telemetry study of 50 squirrels on the rural site, an area with a high risk of predation (Chapter III). On the contrary, squirrels on the urban site had a minimal risk of predation. During a 2-year study overlapping the current study, only one of 78 radio-collared squirrels was preyed upon (Chapter III). I did not conduct a study of predation rates on suburban sites; however, for this study I assumed that the relative amount of predation on a suburban site was less than that on the rural site and more than that of the urban site. Assuming that the effects of human impacts on the ecology of the urban-rural gradient are scaled is reasonable and effective for measuring its results on target populations (Matson 1990, Bowers and Breland 1996).

Observations

To test each of the 3 hypotheses, I collected a minimum of 11 squirrel behavioral observations per site (1 per block, see independent observations section) from January to November 2005. When it was possible to obtain more observations on unused blocks, I did so to increase sample sizes. Observations were performed during periods of high squirrel activity (from 1100 to 1400 hours during fall and summer, and from 1200 to 3000 hours during spring and winter) (Geeslin 1970). Focal squirrels were obtained within a block after the observer had been positioned under a tree for >4 minutes. To reduce the possibility of observing a squirrel's response to the observer or other squirrels, observations were not collected if a squirrel was <30 m away from the observer or if other squirrels were known to be present.

Response to Human Disturbance

To test my first hypothesis, that flight initiation distance and the amount of anti-predator behaviors will decrease and that the types of behaviors will change in response to human approach as the prevalence of humans increases along the rural-urban gradient, I recorded anti-predator behaviors in response to human approach. Squirrels were approached at a constant-paced walk from a distance >30 m. I recorded the distance between the observer and the squirrel when the squirrel fled (flight initiation distance, *approach*). To detect changes in squirrel anti-predator behaviors before and after the human approach, I recorded the number of specific anti-predator behaviors (Table 4.1)

Table 4.1. Description of squirrel anti-predator behaviors and response variables recorded to quantify the impact of human approaches, and hawk and coyote vocalizations across the urban-rural gradient in College Station and Bryan, Texas USA.

Behavior	Variable	Description
Chattering teeth	teeth	Squirrel will chatter teeth rapidly and then, slowing, create a distinct noise.
Scan	scan	On the way up or down a tree, or in the middle of a foraging bout the squirrels will find a vantage point (bench, tree limb) and in a frozen position stare or slowly swivel head from side to side.
Freeze	freeze	Squirrel comes to a stop with hind legs on ground, locking at least one of the two forelimbs on the ground or limb and placing the head above the shoulders. The head will be cocked to the side or face forward.
Freeze upright	freeup	Squirrel comes to a stop with hind legs on the ground or limb and back straight or slightly bent forward. The forelimbs are off the ground.
Tail wag aggressive	tail	The tail moves rapidly snapping back and forth over the head.
Lay down	lay	The squirrel become motionless (usually on a branch) with body and head resting on the same surface.
Response	Variable	Description
Fight initiation distance	approach	The distance from observer to squirrel when the squirrel fled in response to a human approach.
Flush distance (human)	flush	The distance from where the squirrel fled in response to a human approach to where it stopped moving or its distance traveled after 20 seconds.
Flush distance (vocalization)	dis	The distance from where the squirrel fled in response to a hawk or coyote call to where it stopped moving or its distance traveled after 20 seconds.
Freeze response	resfreeze	The amount of time the squirrel froze in response to a hawk or coyote call, not exceeding 20 seconds.
Change in anti predator behavior	anti	The change in the amount of time spent on anti-predator behaviors from before to after a human approach, hawk call, or coyote call.

and the amount of time spent performing these behaviors for a 2-minute interval before and a 2-minute interval 20 seconds after the approach. The amount of time spent on anti-predator behaviors was classified into 1 of 4 categories (0–25%, 25–50%, 50–75% or 75–100%).

I examined the differences between flight initiation distances and changes in the amount anti-predator behavior for non-normal data using logistic regression (PROC LOGISTIC) (SAS Institute Inc. 2002) and examination of graphically represented means and standard errors. To determine overall differences in the types of behaviors displayed across the urban-rural gradient, I used non-parametric discriminate analysis (SAS 1999, Fernandez 2003) to calculate and test differences among Mahalanobis distances. I used non-parametric discriminate analysis because it eliminated the violated assumptions (equal variance, normality) common in the use of discriminate analysis on ecological data (Williams 1983). To select the variables used in the discriminate analysis I used a logistic stepwise regression (entry 0.3, exit 0.4) procedure (PROC LOGISTIC) to remove weak or redundant variables (Klecka 1980).

Habituation

If habituation is a decreased responsiveness caused by repeated exposure to a stimulus (McFarland 1993), then animals from the same habitat and population that have not yet experienced repeated exposure to a stimulus should not show the decreased responsiveness that is displayed by more experienced members of a population. To test my second hypothesis (that reduction in flight initiation distance and anti-predator

behaviors along the urban-rural gradient are due to habituation), I examined the flight initiation distance and anti-predator behaviors of young and adult squirrels on the urban site. To obtain a sample of young squirrels that had not yet been repeatedly exposed to humans, I monitored 33 squirrel nest boxes on the urban site twice a week to determine when young squirrels were weaned and first ventured out of the nest. Within 2 weeks from the time that young squirrels left the nest boxes for the first time I performed a human approach to the young squirrels. In an effort to eliminate temporal bias I also attempted to conduct adult observations during the 2-week periods when the young left their boxes in April and October. Only 1 young squirrel was observed per litter (nestbox) to avoid the possibility of observing an individual twice. I recorded flight initiation distances along with anti-predator behaviors (Table 4.1) before and after the approach of a human on foot, as specified in the previous section. I used logistic regression (PROC LOGISTIC) to examine differences in flight initiation distance and the change in time dedicated to anti-predator behaviors of juvenile and adult squirrels before and after a human approach. In addition, I used stepwise logistic regression (PROC LOGISTIC, entry 0.3, stay 0.4) to identify relevant behaviors and performed non-parametric discriminate analysis (PROC DISCRIM). I calculated Mahalanobis distances and tests of significance of the anti-predator behaviors among juvenile urban, adult urban, suburban and rural squirrels to determine differences in squirrels' anti-predator behaviors and to determine whether juvenile squirrels' behaviors more closely resembled squirrels with less human stimuli experience.

Transfer of Habituation

To test my third hypothesis, that animals habituated to humans show a reduced response to predator stimuli in environments of low predation risk, I exposed squirrels to auditory predator stimuli. After 2 minutes of initial observations of squirrel anti-predator behaviors (procedures and behaviors measured were the same as in the previous section (2)) and ensuring that the squirrel was >30 <50-m away, I played 6 seconds of a recorded vocalization of a red-tailed hawk (*Buteo jamaicensis*) or coyote (*Canis latrans*) to represent the auditory stimuli (Berger et al. 2001) of potential predators (Steele and Koprowski 2001). I recorded the squirrels' response by measuring the number of seconds the squirrel froze (*resfree*) (Table 4.1) and the distance traveled in 20 seconds after the call (*dis*). After 20 seconds, I used the previously established protocol to measure squirrel's anti-predator behaviors for an additional 2 minutes. I used logistic regression (PROC LOGISTIC) to compare the changes in time spent on vigilance behaviors before and after the hawk and coyote vocalizations and represented these changes graphically. Additionally, I explored the similarities and differences in behavioral responses to the hawk and coyote vocalizations across the urban-rural gradient. I used a stepwise logistic regression (PROC LOGISTIC, entry 0.3, stay 0.4) to identify relevant behaviors, conducted a non-parametric discriminate analysis to calculate Manhaloblis distances and tested for significance among all 3 sites.

Results

Response to Human Disturbance

Flight initiation distances were different among sites ($X^2 = 26.33$, $df = 2$, $P < 0.001$) and mean distances were approximately 7 times greater on rural sites (mean = 18.55 m) compared to urban sites (mean = 2.57 m). Graphical representations of means and standard errors suggest an increased trend in average flight initiation distance across the urban gradient, increasing from urban to suburban and from suburban to rural (Figure 4.1). Additionally, changes in the amount of time dedicated to anti-predator behavior in response to human approaches was significantly different among the sites ($X^2 = 10.94$, $df = 2$, $P = 0.004$), with graphical representations of means and standard errors (Figure 4.1) suggesting an increase of about three times the amount of anti-predator behavior from the urban (16%) to the rural sites (56%). A stepwise logistic regression selected *approach*, *lay*, *anti*, and *scan* as relevant variables for differentiating between sites. Using these variables in non-parametric discriminate analysis showed significant differences in behaviors among all of sites ($P < 0.036$) (Table 4.2). Mahalanobis distances of overall differences in anti-predator behavior among the sites were consistent with the urban-rural gradient, with the rural and urban sites being separated by the most distance (5.01 m) and rural and suburban sites separated by the least distance (2.01 m) (Table 4.2).

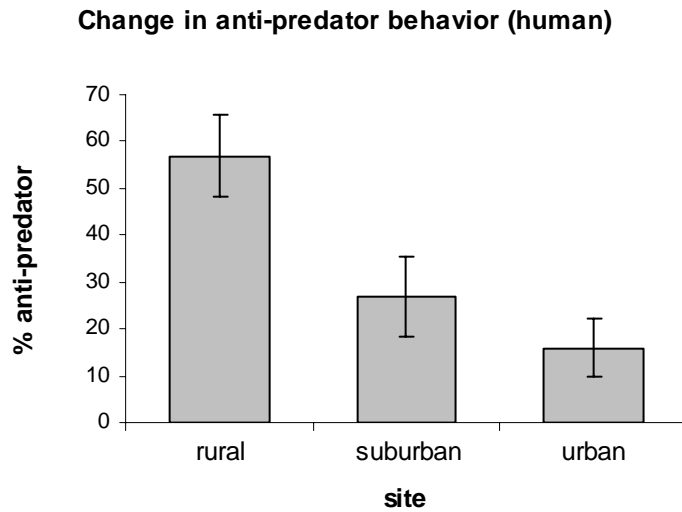


Figure 4.1 Means and standard errors of flight initiation distances and changes in the amount of anti-predator behavior of squirrels in response to human approach across the urban-rural gradient on urban, suburban and rural sites in College Station and Bryan, Texas, USA.

Table 4.2. Manhaloblis distances and tests of significance of squirrel anti-predator behaviors in response to human approach among urban, suburban and rural sites in College Station and Bryan, Texas, USA.

Site	Distance	Urban		Distance	Suburban		Distance	Rural	
		<i>F</i>	<i>P</i>		<i>F</i>	<i>P</i>		<i>F</i>	<i>P</i>
Urban	0	0	0	3.99	6.64	< 0.001	5.01	7.09	< 0.001
Suburban	3.99	6.64	< 0.001	0	0	0	2.01	2.93	0.035
Rural	5.01	7.09	< 0.001	2.01	2.93	0.035	0	0	0

Table 4.3. Manhaloblis distances and tests of significance comparing anti-predator behaviors in response to human approach of juvenile urban squirrels to adult urban, suburban and rural squirrels in College Station and Bryan, Texas, USA.

Site	Distance	Juvenile	<i>P</i>
		<i>F</i>	
Juvenile	0	0	0
Urban	5.98	7.08	< 0.001
Suburban	1.18	1.44	0.23
Rural	1.67	1.76	0.14

Habituation

Flight initiation distances were significantly different between juvenile and adult squirrels on the urban site ($X^2 = 35.89$, $df = 1$, $P < 0.001$). Juveniles had a mean approach distance of 17.75 m while adults had an approach distance of 2.57 m. Changes in the amount of time dedicated to anti-predator behavior between the adults and juveniles was significant ($X^2 = 9.46$, $df = 1$, $P = 0.002$) with juveniles (46%) averaging almost 3 times greater changes in time spent on anti-predator behaviors after a human approach than adults (16%). A stepwise logistic regression selected *approach*, *freeze*, *tail*, *teeth* and *scan* as the most significant behaviors in differentiating among the juveniles, adults, suburban and rural squirrels. Using these variables in a non-parametric discriminate analysis I found a significant difference between urban and juvenile behaviors ($P < 0.001$) but failed to find a significant difference in anti-predator behaviors between juvenile and suburban, and juvenile and rural squirrels (Table 4.3).

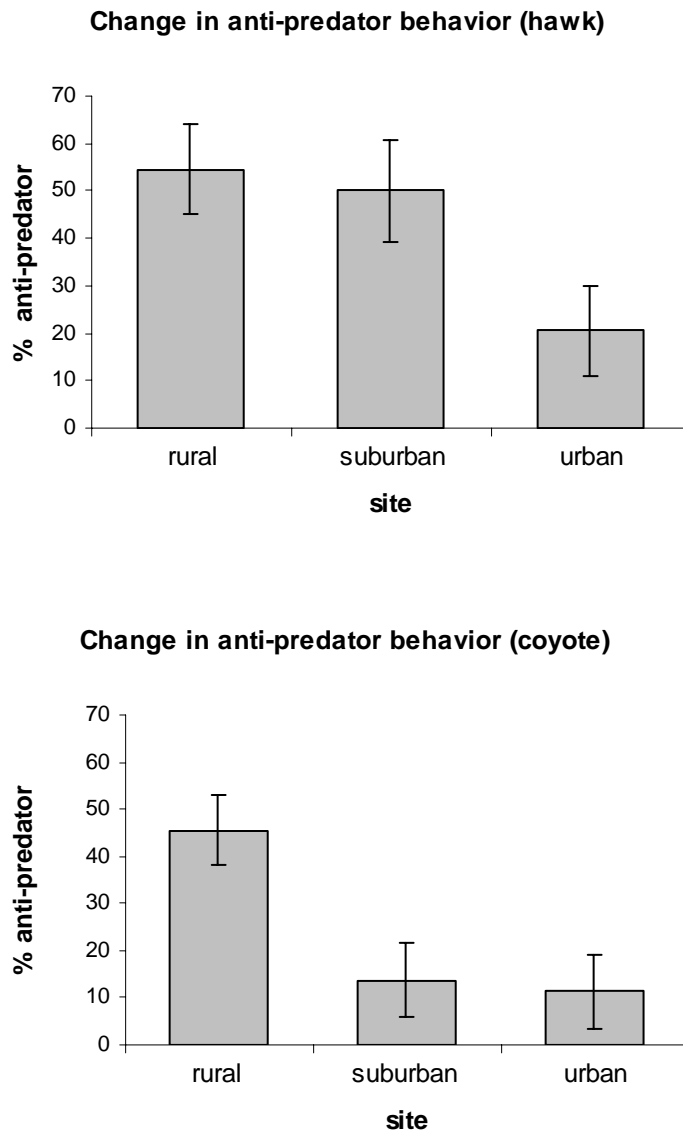


Figure 4.2. Means and standard errors of changes in the amount of anti-predator behavior of squirrels in response to hawk and coyote vocalizations across the urban-rural gradient on urban, suburban and rural sites in College Station and Bryan, Texas, USA.

Transfer of Habituation

Overall changes in the amount of time spent on vigilance behaviors were significantly different among sites for both coyote ($X^2 = 9.83$, $df = 2$, $P = 0.007$) and hawk ($X^2 = 6.50$, $df = 2$, $P = 0.035$) vocalizations. Responses to both vocalizations on rural sites (coyote = 45%, hawk = 55%) measured by the change in time spent on anti-predator behaviors averaged at least twice that found on the urban sites (coyote = 11%, hawk = 20%). Figure 4.2 shows the time dedicated to anti-predator behaviors in response to both hawk and coyote vocalization and shows trends of increasing anti-predator behaviors across the urban-rural gradient, although this trend appears to be less pronounced in response to the coyote vocalization. Stepwise logistic regression indicated that *distance*, *anti* and *freeze* were relevant behaviors for determining differences in responses to the coyote vocalization, while *lay*, *freeze*, *scan*, *tail* and *resfree* were relevant variables in determining differences between the site in response to hawk vocalizations. Tests of manhaloblis distances from non-parametric discriminate analysis of the relevant variables for response to hawk vocalizations indicated significant differences between urban and rural, and urban and suburban sites ($P < 0.04$) but not between suburban and rural sites (Table 4.4). Nonetheless, Manhaloblis distances did increase from the urban site to the suburban site and again to the rural sites. Urban and rural sites differed in response to coyote vocalization ($P < 0.001$) (Table 4.4), however, there was little overall difference (distance = 0.23, $P = 0.75$) between the anti-predator behaviors displayed by the squirrels on the urban and suburban sites.

Table 4.4. Manhaloblis distances and tests of significance of squirrel anti-predator behaviors in response to hawk and coyote vocalizations between urban, suburban and rural sites in College Station and Bryan, Texas, USA.

Predator stimuli	site	Distance	Urban		Distance	Suburban		Distance	Rural	
			<i>F</i>	<i>P</i>		<i>F</i>	<i>P</i>		<i>F</i>	<i>P</i>
Hawk Call	Urban	0	0	0	3.32	3.17	0.023	3.98	3.8	0.01
	Suburban	3.32	3.17	0.023	0	0	0	1.33	1.27	0.31
	Rural	3.98	3.8	0.01	1.33	1.27	0.31	0	0	0
Coyote Call	Urban	0	0	0	0.23	0.4	0.75	4.09	7	<0.001
	Suburban	0.23	0.4	0.75	0	0	0	3.71	6.34	0.002
	Rural	4.09	7	<0.001	3.71	6.34	0.002	0	0	0

Discussion

Response to Human Disturbance

I found that squirrel flight initiation distances and the amount of time spent on vigilance behaviors increased while the types of anti-predator behaviors changed, when the number of human present along the urban-rural gradient decreased. This suggests that squirrels have a mechanism to adjust their behavior and cope with the constant predator stimuli created by humans in urban environments. If squirrels in urban environments had shown a response to humans similar to those in rural areas, they would have spent most of their time and energy on anti-predator behaviors, leaving little time for foraging and reproduction. For example, after an approach of a human within approximately 19 m, rural squirrels on average spent more than 60% of the next 2 minutes performing anti-predator behaviors and, on average, at least 50% of time the squirrel was laying flat and motionless on a branch. Squirrels on the urban site most likely spend a good portion of their life within 18.55 m of humans and did not flee from human approach until they were approximately 3 m away. My study suggests that squirrels have altered their behavior to allow them to better utilize the urban environment. It does not, however, contradict findings that urban wildlife spends more overall time on vigilance than their rural counterparts (Ward and Low 1997, Randler 2003). It is possible that a multitude of lesser behavioral responses in reaction to numerous stimuli outweigh fewer heightened behaviors.

Habituation could explain the reduced response to humans by squirrels. Some studies have shown a reduction in flight initiation distances in animals with greater prior exposure to humans (Knight et al. 1987, Labra and Leonard 1999, Metcalf et al. 2000, Reimers and Sigurd 2001), and one of the most common and highly plausible explanations given for the phenomenon is a reduced response as a result of habituation (Knight et al. 1987, Labra and Leonard 1999, Metcalf et al. 2000, Reimers and Sigurd 2001). An alternative explanation is the rarity principle (Curio 1993) which predicts that prey will respond to rare stimuli more than to stimuli to which they have been regularly exposed. Under this scenario highly lethal predators would elicit a lesser response if prey became more familiar with it. An additional explanation is that the urban environment of minimal predation risk has caused a general reduction in anti-predator behaviors. Researchers believe that animals are able to assess their predation risk and adjust their behaviors (Lima and Dill 1990, Blumstein 2002) and, in the absence of predators, might greatly reduce their use of anti-predator behaviors and recognition of predators (Blumstein 2002). However, the mechanism for such behavioral changes is not clearly specified.

Habituation

I found drastic differences in flight initiation distances and anti-predator behaviors to approaching humans in the responses of juvenile squirrels compared to adult squirrels in the same urban environment. This does support my hypothesis that the reduction of flight distance and vigilance behaviors along the urban-rural gradient is due

to habituation. I assumed that the anti-predator response to humans was innate (Frid and Dill 2002) and that repeated exposure to humans caused a reduction in anti-predator behavior in response. This hypothesis also is supported by my analysis of anti-predator behaviors that showed juvenile squirrels' behavioral responses to be most similar to those of suburban and rural adult squirrels (Table 4.3) that were also presumably not habituated to humans. One flaw of the study design was a lack of a control; undoubtedly, the juvenile squirrels were exposed to humans prior to my observations.

There are several alternative explanations to account for differences in flight initiation distances and behaviors. Again, I was unable to rule out the rarity principle because an approaching human might be rare to a juvenile squirrel and, at the same time, more familiar to adult squirrels. The plausibility of this alternative hypothesis could be reduced by showing that squirrels have stronger reactions to lethal predators that are common, than to harmless animals that are rare. Additionally, it is possible that young squirrels show heightened predator responses that dissipate with age regardless of their amount of exposure to humans. A similar experiment on juvenile rural and suburban squirrels might help clarify this. Nonetheless, I believe that my hypothesis of habituation is the most plausible hypothesis and this experiment provides a basis to begin understanding the mechanisms that influence the behavioral choices of animals on the urban-rural gradient.

Transfer of Habituation

There was a clear reduction in anti-predator behaviors shown in squirrels from urban areas in response to hawk and coyote vocalizations in comparison to rural squirrels. In response to hawk vocalizations the reduction of anti-predator behaviors appeared to be consistent with the urban-rural gradient. However, suburban and urban squirrels showed little difference in their responses to the coyote vocalizations. Nonetheless, my findings do support the hypothesis that habituation to humans may cause a reduction in response to other predator stimuli when there is a minimal risk of predation. This is the first documented case of this phenomenon occurring in a field setting, although it has rarely been tested (Curio 1993, Labra and Leonard 1999), and to my knowledge never tested under the scope of predation risk.

A competing hypothesis presented in the previous response to human disturbance section might also be applicable here. The reduced response to hawk and coyote vocalizations might have resulted solely from the reduced predation risk in the urban environment, rather than a requirement for the transfer of habituation. Nonetheless, this alternative hypothesis does little to explain the differences in response to humans shown between adult and juvenile squirrels in the same environment, or provide an explanation as to how the squirrels might have assessed the risk and altered their behavior.

One explanation for the lack of differentiation between squirrel responses to coyote vocalizations on the urban and suburban sites was that that my assumption of varying predation risk was violated. A competing explanation is that a prevalence of dogs found on the suburban site caused squirrels to habituate to canine vocalizations;

both the urban and suburban squirrels showed little response to the coyote vocalizations. This explanation did not appear to be consistent for hawk vocalizations. Hawks were noticeably abundant on the rural site, less frequently observed on the suburban site, and scarce on the urban site. Squirrels' reactions to hawks also support a rejection of the rarity principle hypothesis, presented in the previous response to human disturbance section. Rural squirrels showed a greater response to a stimulus with which they were likely more familiar than urban squirrels that were rarely exposed to hawks. A final alternative hypothesis is that the squirrels on the urban and suburban sites are exposed to constant noise stimuli to which they have become habituated, and they reacted to the vocalization as they would any noise of the same volume. This hypothesis states that it is not the habituation to humans that has caused a reduced predator response, but rather the anthropogenic noise from the urban environment. To test this, I would need to eliminate the possibility of habituation to humans but not the noise they create, which would be virtually impossible in a field setting.

The study shows a reduction of anti-predator behaviors by squirrels in response to humans and other predator stimuli that in most circumstances is consistent with the urban-rural gradient. It appears clear that the urban-rural gradient does affect squirrels anti-predator behaviors; however, I can only begin to understand how this happens. Further work must be completed to determine the exact mechanisms for these phenomena. Still, I believe the study provides support for the hypotheses that wildlife in urban areas can become habituated to humans and that this reduction in anti-predator behavior can be transferred to other stimuli under the right circumstances.

CHAPTER V

IMPROVING ADDITUDINAL FRAMEWORKS FOR NATURAL RESOURCE CONFLICTS

Synopsis

Attitudinal research of natural resource conflicts have ignored behavioral outcomes or used the theory of reasoned action (TRA) to link attitudes to behaviors; however, research suggest that measures not included in the TRA, such as previous behaviors and accessible attitudes, can improve the link to attitudes and behaviors. My goal was to improve the attitude-behavior link for wildlife and natural resources scientists who might wish to avert negative responses to management decisions. I used a survey to explore the attitude-behavior relationship of a university community, in response to proposals to manage the campus's squirrel population. My data suggests that beliefs and attitudes, modified by variables shown to increase accessibility, generally correspond better to behavioral intentions than unmodified attitudes and beliefs. My data also suggests that the inclusion of a measure of previous behavior shows a strong relationship to behavioral intentions and will increase the predictive ability of models within different theoretical frameworks including the TRA. Most importantly, for the advancement of a comprehensive theoretical framework, my study showed composite models combining components of the TRA and attitude to behavioral process models (ABPMs) out-performed other models.

Introduction

Urban areas have expanded into wildlife habitats and some wildlife populations have adapted to humans and human-altered environments (deer, squirrels, raccoons, geese) (Adams et al. 2006). As a result, there is increased contact and conflict between wildlife and humans (Adams et al. 2005). In addition, citizens in the United States have become increasingly aware and involved in the management of the wildlife surrounding them, usually through participation in non-governmental organizations (NGOs) (Decker et al. 2001). Researchers have responded to increased conflicts and public participation by assessing stakeholders' attitudes in an effort to include public sentiments into wildlife management decisions (Peterson and Manfredo 1993, VanDruff et al. 1996). Unfortunately, the relationship between attitudes and behaviors is not guaranteed and researchers attempting to use attitudes to predict and avert negative outcomes (ballot initiatives, legislative bans, editorials, protests, forced resignations and general political backlash) for the management of wildlife often do not consider exactly how attitudes relate to behaviors (McCleery et al. 2006a).

A handful of researchers studying human-wildlife conflicts (Zinn et al. 1998, Connelly 2002, Campbell and McKay 2003, Fulton et al. 2004, Lauber and Knuth 2004) have addressed the lack of a theoretical framework and generally low correlation between attitudes and behavior (Eagly and Chaiken 1993), by applying the widely used expectancy models, the theory of reasoned action (TRA) (Ajzen and Fishbein 1980) and its variant the theory of planned behavior (TPB) (Ajzen 1991). Both of these models work under the assumption that humans process information and use it to decide how to

act (Ajzen and Fishbein 1980, Fishbein and Manfredo 1992). In the TRA and TPB this cognitive process of behavioral decision, labeled behavioral intentions, is a direct indicator of behaviors to be performed. Behavioral intentions are determined by an individual's attitude toward a behavior and his or her subjective norms (Ajzen and Fishbein 1980). Subjective norms are defined as an individual's perceptions of the social pressures that significant others place on them to perform or not perform a given behavior (Fishbein and Manfredo 1992). Attitudes toward the relevant behavior consist of beliefs about the features of the behavior and beliefs about the consequences of the behavior (Ajzen and Fishbein 1980). For example attitudes about drinking beer would consist of beliefs about beer and beliefs about what happens when you drink beer. The TRA and TPB have shown some degree of success in predicting behaviors and behavioral intentions (Eagly and Chaiken 1993), especially for highly specific behaviors such as cigarette smoking (O'Callaghan et al. 1999), drinking (Conner et al. 2003) and seatbelt use (Stasson and Fishbein 1990). However, there have been numerous theoretical and empirical challenges to the TRA and TPB. Theorists have questioned the idea that behaviors are influenced solely through cognitive processes (Bentler and Speckart 1979, Eagly and Chaiken, 1993, Conner and Armitage 1998), and research has shown that measures of past behaviors, self identify and moral norms can help improve the predictive abilities of expectancy models (Conner and Armitage 1998, Ajzen 2001).

An alternative theoretical approach for linking behaviors to attitudes is the use of attitude-to-behavioral process models (ABPMs). These models have more direct links from attitudes about targets to behaviors than expectancy models. In ABPMs behavior

is influenced by how individuals perceive a situation when they encounter an attitude object (Fazio 1990). These perceptions are a function of activated attitudes toward a target. The more accessible an attitude (the speed with which it can be retrieved to the conscious mind) (Fazio et al. 1982) the greater the chance it has of being activated and influencing an individual's perceptions. In support of this theory, it has been shown that highly accessible attitudes have a stronger link to behaviors than those attitudes that are not as accessible (Fazio et al. 1982). Research has shown that previous experience and knowledge of an attitude object increases accessibility and the link between attitudes and behaviors (Fazio 1990, Eagly and Chaiken 1993). Nonetheless, theorists have suggested that the best use of this link between accessible attitudes and behaviors may not be ABPMs but, instead, incorporating the link it into expectancy models (Eagly and Chaiken 1993, McCleery 2006). In this regard, numerous (Bagozzi and Kimmel 1995, O'Callaghan et al. 1999, Conner and Armitage 1998, Conner et al. 2003) studies have successfully modified the TRA or TPB by including measures of previous behavior. Still, there is a paucity of information on questions that have emerged from the integration of the TRA and ABPMs and the addition of variables to the TRA and TPB; such as, where do previous behaviors fit into the model (Bentler and Speckart 1979) and what is the relationship between behavioral intentions and accessible attitudes?

My goal was to improve the attitude-behavior link for wildlife and natural resources scientists who might wish to avert negative responses to management decisions. Negative responses can be difficult to predict because they cover a wide range of behaviors. An ideal framework for managers would link attitudes about the

resource (wildlife, fish, forest, etc.) and management strategies (harvest, bag limits, clear-cut) to negative behaviors from stakeholders (protests, letters, negative media coverage, etc.). Consequently, I attempted to improve the attitude-behavior link and create a new framework that combined aspects of expectancy models and ABPMs.

I used a survey to explore the attitude-behavior relationship, of a university community, in response to proposals to manage the campus's squirrel population. From survey responses, I determined that poisoning squirrels was the most undesirable option to survey respondents and based my examination of the attitude-behavior link on that management option. I studied 3 different aspects of the relations between attitudes and behaviors: (1) I tested how different variables shown to increase accessibility (knowledge, experience, previous behaviors and involvement in conservation organizations) alter the attitude-behavioral intention relationship, (2) I compared various placements of previous behaviors into the TRA framework and (3) I tested different variants of composite models that included components of the TRA and ABPM models to determine their ability to predict behavioral intentions.

Methods

Research of human-wildlife conflicts has been hindered by an inability to define the relevant behaviors that researchers want to predict (McCleery et al. 2006a). To obtain a measure of the behaviors expected in response to an unpopular wildlife management strategy, I conducted a pretest of 120 individuals. Using open-ended questions I asked participants about the civic behavior they might perform in response to

a proposal to reduce the campus's squirrel population. I generated a list of behaviors that could directly or indirectly hinder the implementation of a management initiative, including; voting, writing letters, calling or e-mailing officials, letters to the editor, signing a petition, attending a protest, organizing a protest, joining or attending meetings of a group opposing the measure and expressing opinions to friends and family members. I used this list to help construct a questionnaire to assess behavioral intention, attitudes, beliefs, attitude accessibility, and social norms related to squirrel management (Appendix I). Using e-mail, I invited 6550 stratified random participants of Texas A&M University undergraduate (3550), graduate (2000), and faculty and staff (1000) populations (College Station, Texas USA) to fill out an electronic version of the questionnaire located on a website. I received 3,154 responses, 2,556 of which were complete and used in hypothesis testing and model comparison (I disregarded 22% undergraduate, 15% graduate, and 16% faculty and staff questionnaires because one or more questions were not completed or responses contained obvious embellishments and jokes).

Variables Used

Behavioral Intention – Behavioral intentions were measured by 2 questions (Cronbach's $\alpha = 0.82$) if 'implemented (squirrel poisoning) would you respond in any way' and an open-ended question 'what would your response be to the management strategies you opposed' (again, squirrel poisoning). Only those respondents who answered that they would respond to poisoning squirrels and then listed at least one of

the civic behaviors identified in the pretest (with the addition of “sabotage”) were considered to have a behavioral intent to act.

Attitudes and beliefs – Attitudes toward behaviors were formed from beliefs about the squirrel population, beliefs about squirrel management techniques and an evaluation of the outcomes of civic behaviors (Ajzen and Fishbein 1980, Francis et al. 2004). I measured beliefs about the squirrel population with 2 questions on a 5-point bipolar scale (Cronbach’s $\alpha = 0.85$): “Which best describes the campus squirrel population (too many – too few)” and “which goal is most appropriate in the management of the campus squirrel population (considerable increase – considerable reduction)”. I assessed beliefs toward squirrel management techniques with 2 measures, “rank from your most to least preferred” and “which would you be least likely to support”. Listed beneath these questions was a list of 6 management options, half the options were aimed at reducing the population and the other half aimed at increasing the population. I checked the measures for internal consistency (Cronbach’s $\alpha = 0.91$) and used the measure of rank to represent the beliefs of management techniques. I measured beliefs towards the outcomes of 10 civic behaviors on a 5-point bipolar scale (very negative – very positive) and summed the results. Participants were asked to evaluate writing letters to the editor, letters to officials, attending a protest, placing a call to an official, signing a letter or petition, criticizing officials, attending meetings to change public decisions, laws or regulation you disagree with and expressing opinions on a public decision to friends and family members. From beliefs I constructed overall attitudes about performing civic behaviors in response to squirrel poisoning. To

generate attitudes for the TRA I multiplied the values obtained for beliefs about the squirrel population and beliefs about squirrel management techniques by the evaluation of civic behavior and summed the results (Francis et al. 2004).

Subjective norms – Subjective norms were comprised of 2 measures: “How would the people who are most important to you view your response (decision to perform a civic behavior; very negatively – very positively)” and “describe the support for your response from the people most important to you (strongly discourage – strongly encourage)”. I assessed both questions on a 5-point bipolar scale and summed the scores (Cronbach’s $\alpha = 0.80$).

Accessibility and previous behaviors – I assessed various measures shown to increase the accessibility of attitudes. I collected additional variables for beliefs toward the squirrel population, beliefs toward management techniques used on squirrel populations and evaluation of civic behaviors. I assessed *experience* with regard to the squirrel population with 2 questions “within the last 12 months about how many times have you talked about the squirrels on the campus” and “within the last 12 months about how many times have you talked about squirrels” (none, 0–5, 5–10, 10–15 or 15–20). I summed the scores (Cronbach’s $\alpha = 0.90$) and created 10 categories of experience. I assessed *knowledge* of the squirrel population by asking participants to describe their knowledge of squirrels if they were “talking to someone they did not know” on a 10-point scale (no knowledge – comprehensive knowledge). I formulated 3 measures of accessible beliefs based on *experience* and *knowledge* and a combination of the 2 by multiplying squirrel population beliefs by *experience* and *knowledge* and then summing

the scores for the combined measure. I measured *experience* (direct and indirect experience) and *direct encounter* of squirrel management techniques by asking respondents how many of 6 listed management strategies they were familiar with and how many of the 6 had they “personally been involved with”. Again, the measures were multiplied by beliefs (squirrel management techniques) to achieve accessible beliefs based on *experience*, *direct encounter* and a combination of the 2. I measured *involvement* as a possible mediator of evaluations of civic behaviors as the number of hours spent per week (none, 1–2, 2–3, 4–5, more than 5) active in a formal conservation, animal welfare oriented or natural resource advocacy organizations. To measure *previous behaviors* I asked respondents to check off any of 10 civic behaviors they had performed in the last 12 months and any of the 10 civic behaviors they had performed in relation to wildlife or natural resources. I summed the 2 questions (Cronbach’s $\alpha = 0.6$) and grouped them into 5 (20 percentile) groups. *Involvement* and *previous behaviors* were multiplied by evaluations of civic behaviors to obtain accessible beliefs based on *involvement*, *previous behaviors* and a combination of the 2. In addition, I used the measure of *previous behaviors* separately as a measure with a direct pathway to behavioral intention.

Statistical Analysis

In each of the following 3 parts of this study, I used SAS Institute (1999) software to assess the relationships among variables and the fit of causal models aiming to predict behavioral intentions. Behavioral intentions were represented as a binomial

(intend to behave/do not intend to behave) and thus all regressions performed were binomial logistic regressions. I compared the fit of models (descriptions of models follow in subsequent sections) using likelihood ratio tests and Akaike's information criteria corrected for small sample size (AICc), which adjusts for the number of parameters used in the models (Simonoff 2003). The model with the lowest AICc value was considered the best approximating model of the data and the best fit of the data. Models with an AICc value <2 of the best models' AICc were also considered competing models. If the AICc value of the model was >4 from the best approximating model it was not considered a plausible explanation of the data (Burnham and Anderson 1998). Additionally, I used a Wald test (Simonoff 2003) to examine the fit of individual parameters within the models shown to best approximate the data.

Part I

Studies have clearly shown that experience with an attitude object increases an attitude's ability to predict behaviors (Fazio and Zanna 1981, Fazio et al. 1982). One explanation for the increased predictability of accessible attitudes is that experience makes attitudes more accessible and more likely to be evoked in the presence of an attitude object, in turn, making them more likely to relate to relevant behaviors (Fazio 1990). There is also evidence that knowledge of an attitude object increases the relationship between attitudes and behaviors (Kallegren and Wood 1986), again possibly because of increased accessibility (Fazio 1986).

In natural resources conflicts, stakeholders have varying degrees of experience with and knowledge of resources (Decker et al. 2001) that should mediate the impact of their attitudes on behaviors. I tested whether including measures of experience, direct encounter, knowledge and previous behaviors increased the predictive relationship between attitudes and behavioral intentions. Additionally, there is a strong trend in wildlife and conservation activism for individuals to become active in local organizations and NGOs (Decker et al. 2001). Following the logic of Eagly and Chaiken (1993) that more input or relevant information given to attitudes strengthens their correlation with behaviors, and the suggestion of social scientists working on natural resource issues (Campbell and McKay 2003, McCleery et al. 2006a) that group affiliation and participation should increase the predictive qualities of attitudes, I also wanted to determine if a measure of involvement in conservation organizations and NGOs would increase the link from attitudes to behavioral intentions.

Hypothesis

I hypothesized that measures of experience, knowledge, direct encounter, previous behaviors and involvement in conservation based organizations would all increase the relationship between attitudes and behavior intentions. In addition, I believed the strongest relationships among attitudes and behavioral intentions would be shown by attitudinal variables that combined the measure of experience, knowledge and involvement.

To test these hypotheses, I evaluated the relationships between beliefs and behavioral intentions for accessible and unmodified beliefs as described earlier. I tested 3 sets of variables comprised of the beliefs that were incorporated into a measure of overall attitudes (beliefs toward the squirrel population, beliefs toward squirrel management techniques and evaluations of civic behaviors) by correlating them with behavioral intentions. Each set of variables included a measure of the belief and 3 measures of the beliefs modified by the measures of accessibility as described earlier.

Results and Discussion

All 3 sets of variables offered varying degrees of support for my hypothesis that measures of multiple accessibilities would improve the relationship of attitudes to behavioral intentions. *Experience* and *knowledge* of the squirrel population increased the correlation between beliefs and behavioral intention (Table 5.1). Additionally, the combined measure of *experience* and *direct encounter* helped to increase the correlation of beliefs of squirrel management techniques (Table 5.1). The addition of a measure of *direct encounter* alone actually reduced the correlation between beliefs and behavioral intentions, yet when combined with a measure of *experience* it was the best variable for predicting intentions. Few participants reported many encounters with the wildlife techniques described in the survey, possibly limiting direct encounter's usefulness as a stand-alone measure of accessibility.

Previous behaviors also increased the correlation between evaluations of civic behaviors and behavioral intentions. This is consistent with research suggesting a strong

Table 5.1. Likelihood ratios and AICc (Akaike information criteria corrected for small sample size) values for logistic regressions of beliefs and beliefs modified by variables to increase accessibility against behavioral intentions to act.

Beliefs	Accessibility variables	Likelihood ratio	<i>p</i>	-2 loglikelihood	AICc
Squirrel population	none	105.49	< 0.0001	2424.06	2430.91
	knowledge	174.87	< 0.0001	2354.65	2361.42
	experience	184.96	< 0.0001	2344.56	2351.32
	knowledge and experience	220.05	< 0.0001	2309.47	2316.19
Squirrel management	none	126.79	< 0.0001	2402.73	2409.56
	experience	140.26	< 0.0001	2389.27	2396.08
	direct experience	78.3	< 0.0001	2451.22	2458.11
	direct experience and experience	151.79	< 0.0001	2377.73	2384.53
Evaluation of civic behaviors	none	142.60	< 0.0001	2386.92	2393.73
	previous behaviors (PB)	267.01	< 0.0001	2262.52	2269.18
	Involvement	91.35	< 0.0001	2438.17	2445.04
	PB and involvement	197.57	< 0.0001	2331.95	2338.69

relationship between past behaviors and attitudes (Conner and Armitage 1998). Nonetheless, involvement in conservation and wildlife organizations actually reduced the correlation of behavioral evaluation with behavioral intentions. Undergraduates were proportionally more involved with these organizations. Still, the relationships did not change when I controlled for occupation (undergraduate student, graduate student, faculty and staff). Campbell and McKay (2003) showed that organizational or group affiliation helped predict social norm in a natural resources management context, however; my data suggests that measuring involvement in a conservation organization as a mediator of beliefs does not add to the prediction of behavioral intentions contradicting McCleery et al. (2006). This may indicate that group involvement has little or no impact on behavioral intentions as a modifier of behavioral evaluations; however, it is also possible that group involvement has a more direct impact on behavioral intention or modifies another predictor of behavioral intentions. Nevertheless, my results offer support for the hypothesis that measures of experience, knowledge, direct encounter, and previous behaviors improve the relationship between attitudes and behavioral intentions.

Part II

Part I of my study suggested that previous behaviors increased the relationship between attitudes and behavioral intentions. Other researchers have suggested that, within the framework of the TRA, previous behaviors should have a direct link to behaviors and behavioral intentions along with a link to attitudes (Bentler and Speckart

1979). The mechanism by which previous behaviors influences behavioral intentions and future behaviors is still unclear, (Conner and Armitage 1998) but the direct link from previous behaviors to behavioral intention and behaviors within the TRA and TPB has been supported empirically by a number of studies in a variety of different contexts (Bentler and Speckart 1979, Bentler and Speckart 1981, Conner and Armitage 1998, Leone et al. 1999, O'Callaghan et al. 1999). In 11 studies, Conner and Armitage (1998) found that in addition to attitudes, subjective norms and perceived behavioral controls (a variable in the TPB), previous behaviors accounted for an additional 7.2% of the variance in behavioral intentions. Despite these findings, theoretically there is more justification to use previous behaviors as a modifier of attitudes (Fazio and Zanna 1981). I know of no study comparing the overall performance of models using previous behaviors as a modifier of attitudes or models using previous behaviors as a modifier of behavioral intentions.

Hypothesis

I hypothesized that previous behaviors would not only influence behavioral intention through attitudes but also directly. I tested 3 models (Figure 5.1) to determine which provided the best overall predication of behavioral intentions using previous behaviors within the TRA framework. In the models, TRA was comprised of a measure of social norms and a measure of overall attitudes about performing civic behaviors in response to squirrel poisoning. These overall attitudes contained beliefs about the squirrel population, beliefs about squirrel management techniques and evaluations of

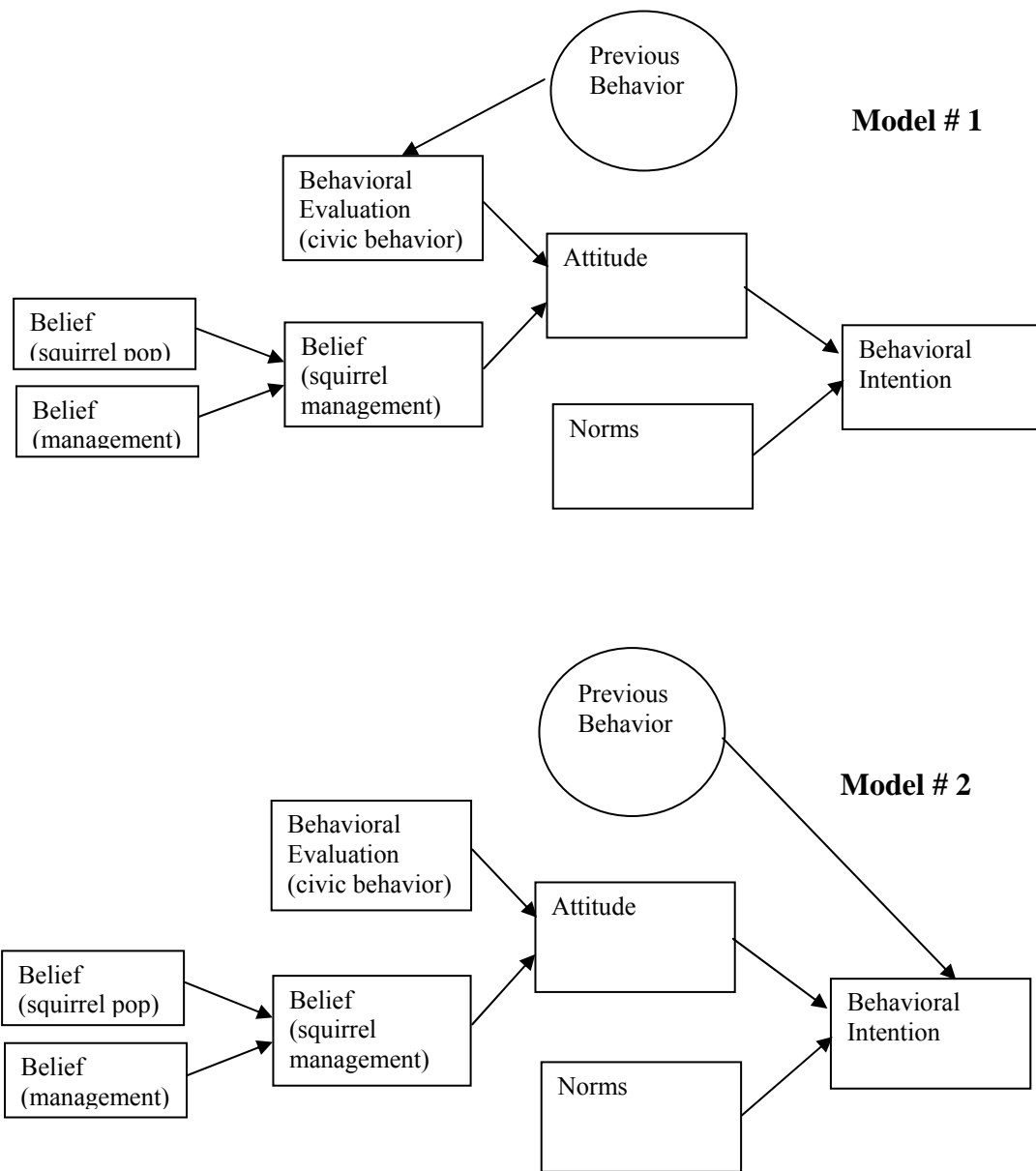


Figure 5.1. Comparison of 3 models with different placements of a measure of previous behaviors within the TRA framework.

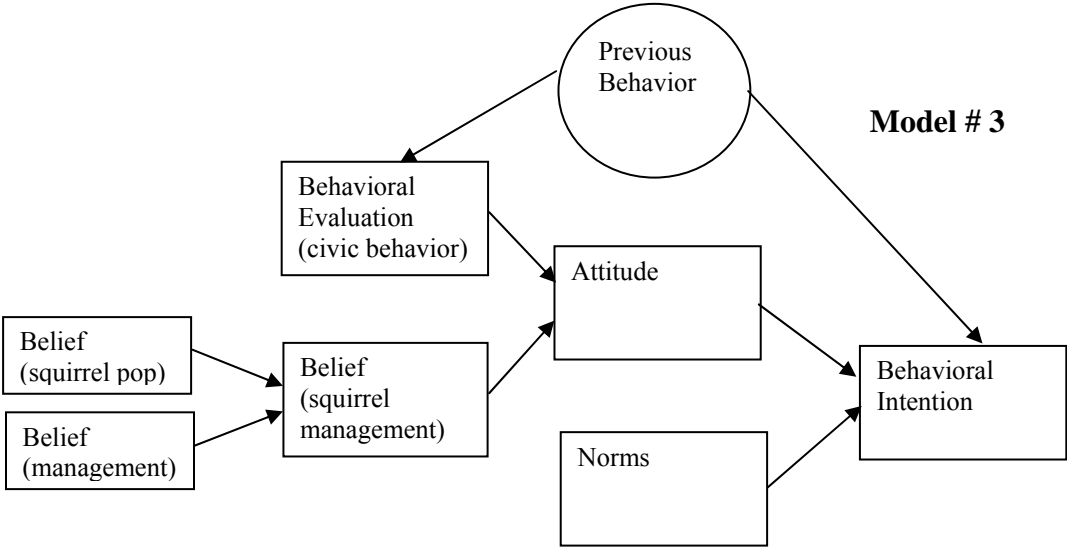


Figure 5.1. (Continued)

civic behavior as described earlier. Model 1 (Figure 5.1) represented the TRA with previous behavior modifying overall attitudes by its inclusion into the measure of behavioral evaluation. Model 2 (Figure 5.1) represented the TRA with previous behaviors separated from attitudes and having a direct pathway to behavioral intentions. Finally, model 3 (Figure 5.1) represented a combination of the previous 2 models with previous behaviors modifying attitudes through behavioral evaluations and having a direct pathway to intentions within the TRA framework. Model 1 should show the greatest explanation of the data if previous behaviors had a direct affect on attitudes and little additional direct influence on intentions. If previous behaviors influenced attitudes and also had a direct link to behavioral intentions my data should indicate that model 3 was the best explanation of behavioral intentions. Alternatively, if previous behaviors directly affected behavioral intention with little additional direct influence on attitudes than model 2 should provide the best explanation of intentions.

Results and Discussion

Model 2 accounted for the most variability in the data and had an AICc score <45 than the other models (Table 5.2). These results clearly rejected my hypothesis that previous behaviors would not only influence behavior intention through attitudes but also directly. From the results in Part I of the study my data indicated that previous behavior increased the relationship of attitudes to behavioral intentions; however within the TRA my data from part 2 of the study indicates that the most influential relationship for previous behaviors is directly with behavioral intentions.

It has been argued that statistical associations between past and future behaviors represent other factors influencing both previous behaviors and future behaviors (Ajzen 1991, Eagly and Chaiken 1993). This rebuttal does not appear to apply to my models because past behaviors influenced behavioral intentions, not future behaviors. I believe the link from previous behaviors to intentions represents a logical association for situations similar to the one I evaluated. In my study the behaviors examined were probably not occurring with any great frequency and had likely not become habitual and capable of affecting behavior without cognition through behavioral intentions.

Table 5.2. Comparison of 3 models ability to predict behavioral intention with different placements of a measure of previous behaviors within a TRA framework. Models were compared using logistic regression and measured with Likelihood ratios and AICc values (Akaike information criteria corrected for small sample size).

Model	Likelihood ratio	<i>p</i>	<i>k</i>	-2 loglikelihood	AICc
1. TRA ^b with beliefs modified by previous behaviors	508	<0.0001	3	2021.52	2030.70
2. TRA ^b , previous behaviors	596.91	<0.0001	4	1932.61	1944.41
3. TRA ^b with modified behavior, previous behaviors	549.33	<0.0001	4	1980.2	1992.10

^b TRA included 2 variables, normative beliefs and attitudes toward behaviors
K = number of parameters in model

It is possible that the effects of previous behaviors on behavioral intention could be mediated by including a measure of perceived behavioral control (a measure found in the TPB) (Ajzen 2001). Nonetheless, it has been shown that the inclusion of this variable does not eliminate the affects of previous behaviors on intentions (Conner and Armitage 1998). Logistics is another factor to consider before adding a measure of perceived

behavioral controls. Generating a measure of behavioral control for a large number of varying behaviors of interest, such as the behaviors examined in this study, could be both cumbersome and difficult. For these reasons when using the TRA framework I advocate the inclusion of previous behaviors with a direct link to behavioral intentions.

Part III

In the first 2 parts of this study my data indicated that increasing information and accessibility of attitudes and introducing a measure of previous behaviors may help to increase the correlation of beliefs to behavioral intention. For the final portion of the study, I wanted to determine if these findings could be used in composite models that included aspects of the TRA and APBMs. In particular, I wanted to test whether activated beliefs had a more direct influence on behavioral intentions than the attitudes towards behaviors, used in the TRA and TPB. Additionally, I wanted to investigate whether attitudes were essential for understanding the relationship between individuals and their intentions. By removing frameworks that included attitudes, I hoped to determine how important they were to the prediction of behavioral intentions.

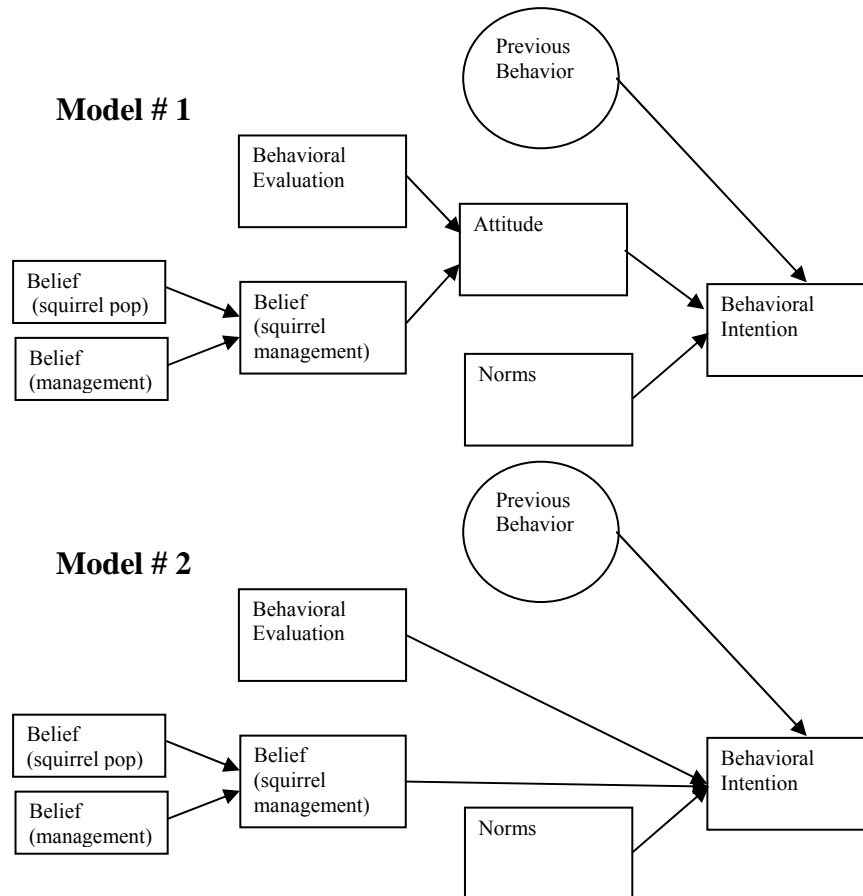


Figure 5.2. Comparison of 5 models with different pathways from beliefs and attitudes to behavioral intentions.

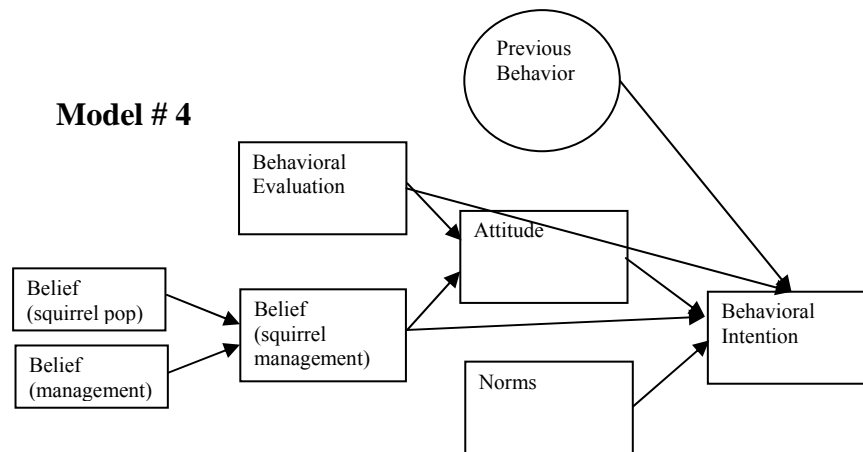
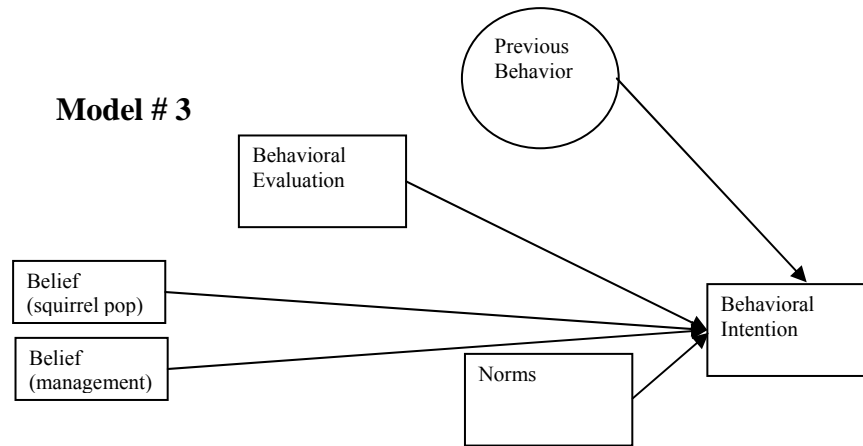


Figure 5.2. (Continued)

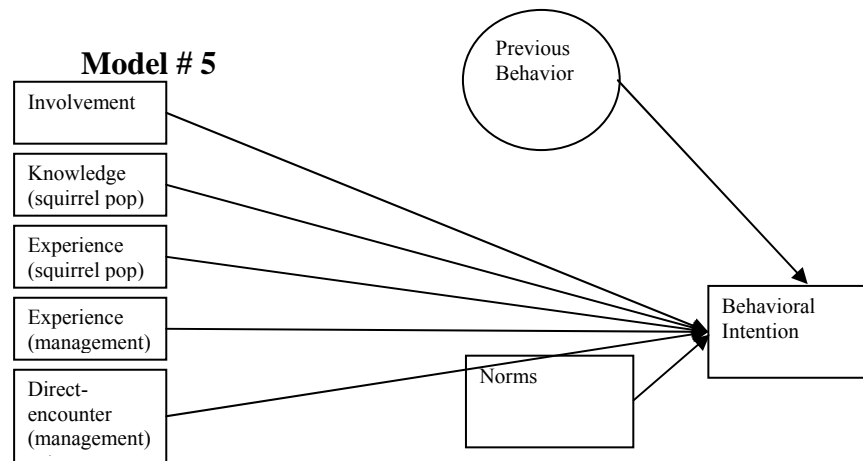


Figure 5.2. (Continued)

Hypothesis

I hypothesized that models including accessible beliefs about the squirrel population and management techniques that were modified by experience, previous behaviors and knowledge would yield better explanations of the data when they had direct pathways to behavioral intentions compared with models that had less direct pathways. I also examined a second hypothesis that beliefs and attitudes improved the relationship between behavioral intentions and information about experiences, previous behaviors and knowledge. I used the survey data to test 5 different models (Figure 5.2) comprised of different pathways from activated beliefs to behavioral intentions from previous experience and information to behavioral intentions. All the models used a structure similar to that of the TRA, where variables were related to behavioral intentions. Similarly, each model contained a measure of social norms and previous behaviors linked solely to behavioral intentions (as suggested from part 2). In the first 4 models (Figure 5.2) I used measures of the participant's beliefs toward the squirrel population that included measures of *experience* and *knowledge* and measures of *experience* and *direct encounter* for beliefs on management techniques. Again, I used the term TRA to indicate that a model has a measure of social norms and a measure of overall attitude comprised of beliefs about the squirrel population, beliefs about squirrel management techniques and evaluations of civic behaviors. Model 1 (Figure 5.2) represented the TRA with the addition of previous behaviors as a modifier of behavioral intentions. Models 2 and 3 (Figure 5.2) are different representations of more direct linkages of accessible beliefs. Model 2 represented accessible beliefs about the target (managing the squirrel population using poison), behavioral evaluations, norms and

previous behaviors with direct pathways to behavioral intention. The relations in Model 3 were even more direct with accessible beliefs about the squirrel population, accessible beliefs about managing squirrels, behavioral evaluations, norms and previous behaviors with direct pathways to behavioral intention. Model 4 (Figure 5.2) was a comprehensive model to ensure that the inclusion of extra variables was not biasing model results. Model 4 represented the TRA with the addition of accessible beliefs about the target, behavioral evaluations and previous behaviors all directly linked to behavioral intentions. In Model 5 there were no beliefs or attitudes in the model. Instead the model was comprised of the measures of *experience* and *knowledge* of the squirrel population, measures of *experience* and *direct encounter* with squirrel management techniques, and measure of *involvement* in conservation related organizations along with social norms and previous behaviors all directly linked to behavioral intentions.

Results and Discussion

In support of my first hypotheses (models with accessible beliefs and direct pathways to behavioral intention provide the better explanations of behavioral intentions than models with less direct pathways) Models 2 and 3 appeared to yield the best approximations of the data (Table 5.3). Model 2 had an AICc value < 0.2 of Model 3 (Table 5.3) indicating that although Model 2 had the lowest AICc value, Model 3 should also be considered as a competing model for best approximating the data (Burnham and Anderson 1998). Each of the variables used in the both Models 2 and 3 were significant ($\alpha < 0.02$) in explaining variance in the data (Table 5.4). In both models previous behaviors and then norms accounted for more variance than the other variables. In

contrast to the TRA's focus on attitude towards behaviors not targets, I found that when evaluations of behavioral outcomes were separated from attitudes toward behaviors they were weak predictors in both models (weakest predictor in model 2, second weakest predictor in model 3) (Table 5.4). These findings help to support some of the theoretical claims of ABPMs that attitudes toward targets influence behaviors when they are accessible. I contend that there is a logical connection from accessible beliefs to intentions, where accessible beliefs influence cognitive behavioral intentions, not simply my attitude toward the behavior itself. For example, the strong belief that I need more squirrels (held by an individual with ample experience and knowledge) should at least, in part, impact their decision to behave against a strategy to reduce the squirrel population. This direct link is diluted when beliefs are incorporated into attitudes toward behaviors without being weighted.

It has been suggested that ABPMs, which hold more direct links from attitudes towards targets to behaviors, breakdown in their explanations of the proximal causes of behaviors (Eagly and Chaiken 1993). However, by using the distal portion (attitude activation) of these models and incorporating them into a framework that stresses a cognitive process, I have at least shown that the TRA and ABPMs can be successfully combined to produce a model with an increased ability to predict behavioral intentions.

Model 5, void of information on beliefs and attitudes, proved to be the least likely model to explain behavioral intentions. Even though my results showed norms and previous behaviors to be the 2 most relevant variables for predicting behavioral intention my results did support my second hypothesis that beliefs and attitudes improved the relationship between prior information about experiences and behavioral intention. It appears that although relevant information and more direct linkages can make beliefs more effective predictors of intentions that the same relevant information used without beliefs is not nearly as affective at predicting behaviors.

Table 5.3. Comparison of 5 models ability to predict behavioral intention with different pathways from beliefs to intentions and from experience to intentions. Models were compared using logistic regression and measured with likelihood ratios and AICc values (Akaike information criteria corrected for small sample size).

Model	Likelihood ratio	<i>P</i>	<i>k</i>	-2 loglikelihood	AICc
1. TRA ^b with modified behavior, previous behaviors	596.91	<0.0001	4	1932.61	1944.41
2. Squirrel beliefs ^a + management beliefs, norms, previous behaviors, behavioral evaluations	645.19	<0.0001	5	1884.33	1898.79
3. Squirrel beliefs ^a , management beliefs, norms, previous behaviors, behavioral evaluations	647.75	<0.0001	6	1881.77	1898.97
4. TRA ^b , squirrel beliefs ^a + management beliefs, previous behaviors, behavioral evaluations	645.48	<0.0001	6	1884.04	1901.25
5. Previous behaviors, norms, experience (squirrels), knowledge (squirrels), experience (management), direct encounter management, involvement	599.27	<0.0001	8	1930.25	1953.13

^a denotes the variable was modified by variables that increased its accessibility

^b TRA included 2 variables, normative beliefs and attitudes toward behaviors

K = number of parameters in model

Table 5.4. Estimates, standard error (SE), and Wald statistics of the variables used in 2 models that best approximated behavioral intentions.

Model	Variable	Estimate	SE	Wald test	p
2. Squirrel beliefs ^a + management beliefs ^a , norms, previous behaviors, behavioral evaluations	norms	0.445	0.043	108.030	<0.0001
	previous behavior	0.289	0.027	112.960	<0.0001
	squirrel beliefs ^a + management beliefs ^a	0.183	0.019	89.580	<0.0001
	behavioral evaluations ^a	0.052	0.011	24.910	<0.0001
3. Squirrel beliefs ^a , management beliefs ^a , norms, previous behaviors, behavioral evaluations	norms	0.439	0.043	104.590	<0.0001
	previous behavior	0.306	0.028	121.070	<0.0001
	squirrel beliefs ^a	0.028	0.003	68.771	<0.0001
	management beliefs ^a	0.009	0.003	6.334	0.0118
	behavioral evaluations ^a	0.053	0.011	25.743	<0.0001

* TRA included 2 variables, normative beliefs and attitudes toward behaviors

^a denotes the variable was modified by variables that increased its accessibility

Overall Discussion

To address conflicts involving the management or manipulation of natural resources researchers have often chosen to study the attitudes of stakeholders (McCleery et al. 2006a). To make attitudinal research more relevant, consistent and applicable studies should be conducted within a theoretical framework (Decker et al 2001, McCleery et al. 2006a). However, the popular frameworks of the TRA and TPB may not be the best models for predicting a range of unseen behavioral responses to a management action. The TRA and TPB frameworks are limited because they use attitudes toward behaviors to predict behavioral intentions and in studies with a multitude of attitudes toward a number of possible behaviors, the implementation of these models could become laborious. Additionally, these frameworks do not provide a direct linkage from attitudes toward targets to behaviors. As an alternative, I suggest models that include measures that influence the accessibility of beliefs and measures of previous behaviors both with direct pathways to behavioral intentions.

My data suggests that beliefs and attitudes modified by variables shown to increase accessibility generally correspond better to behavioral intention than unmodified attitudes and beliefs. My data also suggests that the inclusion of a measure of previous behaviors will demonstrate a strong relationship to behavioral intentions and will increase the predictive ability of models within different theoretical frameworks including the TRA. Most importantly, for the advancement of a comprehensive theoretical framework, my study showed that composite models combining components of the TRA and ABPMs out-performed other models. When I evaluated models with

accessible beliefs separated from attitudes toward behaviors, where beliefs were given direct pathways to behavioral intention, they proved to be better predictors of intentions than models using attitudes towards behaviors. Certainly, these models need refinement but they do show potential as an alternative to the TRA and TPB.

My data supports other research (Conner and Armitage 1998) suggesting a measure of past behavior is helpful in predicting behavioral intention but does little to explain why this is so. To understand how previous behaviors impact intention, I advocate the testing of other variables, in addition to perceived behavioral controls such as temporal stability (Ajzen and Fishbein 2000), affect and knowledge of relevant behaviors (Conner and Armitage 1998), to see whether they can explain the influence of previous behaviors and be incorporated into a more complete model of the attitude-behavior relationship. I believe the further examination of the properties of attitudes, accessibility of beliefs and the relationship of previous behaviors to behavioral intentions can help to modify and build on models utilizing 2 proven methods of linking attitude to behaviors, expectancy models and ABPMs. These advancements in theory can then be used to help managers make better-informed decisions about stakeholders and the public acceptance or rejection of potential management actions.

CHAPTER VI

CONCLUSIONS

Studying fox squirrel ecology has provided useful information on how urban wildlife adapts to urban environments. Adaptations to the urban environment were evident in fox squirrels' altered habitat selection, survival rates and behaviors relative to their rural counterparts. Additionally, by examining the relationship between attitudes and behaviors, I have created a theoretical framework that will allow researchers to more accurately predict and hopefully avert contentious wildlife management programs in the urban environment.

The examination of fox squirrel habitat use in an urban environment suggested that urban fox squirrels have been able to adapt to urban areas. Fox squirrels made the most of the large mast bearing trees that mimicked the habitat features they prefer in non-urban areas, while managing to use, tolerate or avoid the numerous non-native and man-made features of the urban environment. For example, fox squirrels selected to use the inside of buildings within their core areas during the winter and spring when inactive, and non-native grass areas during periods of activity in the fall and spring. Additionally, during periods of activity, fox squirrels avoided using pavement but did not exclude it from their core area movements. This ability to tolerate pavement in core area movements and to use buildings makes vast areas of the urban environment available for fox squirrels to exploit. I was unable to simplify and explain fox squirrel

activity with a few variables, indicating that numerous features of the urban landscape influenced this activity.

A study of fox squirrel survival rates suggested that the rates of survival and causes of mortality between differed between populations of urban and rural fox squirrels. At least 60% of the mortalities on the rural site were caused by predation, while <5% of the mortalities on the urban site were caused by predation. Most of the mortalities on the urban site (>60%) were caused by vehicular collisions. In addition it appeared that sex and seasonality affect survival rates of urban, but not rural, squirrels. What appears clear from this portion of the study is a need to study urban wildlife and their population dynamics separately from their rural counterparts. I have shown differing survival rates in an urban population, but it is unclear how sex ratios, age structures and densities in an urban population may also differ.

Some of the most interesting findings in this dissertation came from examining differences in anti-predator behaviors of squirrel populations across the urban-rural gradient. I found that squirrel flight initiation distances and the amount of time spent on vigilance behaviors increased, and the types of anti-predator behaviors changed as the number of humans present along the urban-rural gradient decreased. This suggests that squirrels have a mechanism to adjust their behavior and cope with the constant predator stimuli created by humans in the urban environment. I also found that adult and juvenile squirrels in the urban environment reacted differently to approaching humans. Juveniles showed a greater flight initiation distance and use anti-predator behaviors longer than adult squirrels. Urban juvenile squirrel behaviors were more closely aligned with

suburban and rural adult squirrels. I believe this provides evidence for a commonly held, but untested, hypothesis that increased contact with humans causes animals to habituate to them. My results also suggest that a potential outcome of habituation to humans may be a transfer of a reduced anti-predator response to other predator stimuli. Fox squirrels on the urban study site showed a reduced response to red-tailed hawk and coyote calls compared with rural squirrels. This was the first documented case of a transfer of habituation occurring in a field setting, possibly because it occurred in a setting with a low risk of predation. The concept of habituation transfer could prove useful in the management of urban species or those wildlife with significant amounts of human contact.

It is almost imperative that work on wildlife in an urban setting include some way of understanding or predicting the response of the stakeholders in direct proximity to the wildlife. I tested several models aimed at improving the prediction of behavioral intentions from attitudes in response to a contentious management proposal. Data from the study suggested that beliefs modified by variables shown to increase accessibility generally correspond better to behavioral intentions than unmodified beliefs. My data also suggested that the inclusion of a measure of previous behaviors helps strengthen the relationship of attitudes to behavioral intentions and helps to increase the predictive ability of models within different theoretical frameworks. Most importantly for the advancement of a comprehensive theoretical framework, the study showed that composite models combining components of the theory of reasoned action (TRA) and attitudes to behavioral process models (ABPMs) out-performed other models. I believe

this study can provide a basis for the continued exploration of the attitude-behavioral link and has provided a clear usable model for dealing with potential contentious issues that can arise from the management of urban wildlife.

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APPENDIX I

Appendix I. Questionnaire and possible responses to a survey given via the internet to students, faculty and staff at Texas A&M University, College Station, TX., USA.

Attitudes towards squirrel and squirrel management on the Texas A&M University campus

The fox squirrel is a common, large tree squirrel with reddish, rust or brown coloration and found in many urban areas. The Texas A&M University Department of Wildlife and Fisheries Sciences (WFSC) has been conducting research on the campus fox squirrel population for 4 years now. Before making a recommendation for the management of the squirrel population, the WFSC would like input from students and the campus community. In the following questionnaire we will be asking you questions about the campus squirrel population and 6 techniques for managing the squirrels. The 6 management techniques are as follow:

- 1) Placing rodent poisons around campus to reduce the population.
- 2) Trapping squirrels, sedating and euthanasia them with an injection.
- 3) Live trapping a portion of the squirrels in cage traps and transferring them to the area in and around Lick Creek Park, in an effort to reduce the population.
- 4) Increasing the number of nest boxes on campus. There are currently 32 wooden nest boxes placed in trees around campus that squirrels use for nests. Increasing the number of nest boxes might increase the number of squirrels
- 5) Installing squirrel crossing signs in an attempt to reduce road mortalities of squirrels. The signs are intended to slow cars since our research has shown that most squirrel mortalities on campus are from road kills.
- 6) Installing official squirrel feeding stations around campus. Increasing the food available to squirrels has the potential of increasing the population.

Please answer the following questions to the best of your knowledge. There are some open ended questions where you are asked to answer the question in your own words. Thank you for your input.

Question 1) Indicate which statements best represents your feeling about size of the Texas A&M fox squirrel population.

(too few – too many)

Question 2) Which goal do you believe would be most appropriate in the management of the Texas A&M squirrel population.

(considerable reduction – considerable increase)

Question 3) Please RANK the management strategies from your most to least referred option (1 most preferred, 6 least preferred).

(Placing rodent poisons around campus)

(Trapping squirrels and sedate and euthanasia them)

(Trapping a portion of the squirrels and transferring them to Lick Creek Park)

(Increasing the number of nest boxes on campus)

(Installing squirrel crossing sign in an attempt to reduce road mortalities of squirrels)

(Installing official squirrel feeding stations around campus)

Question 4) which management strategy would you **least** likely support?

(Placing rodent poisons around campus)

(Trapping squirrels and sedate and euthanasia them)

(Trapping a portion of the squirrels and transferring them to Lick Creek Park)

(Increasing the number of nest boxes on campus)

(Installing squirrel crossing sign in an attempt to reduce road mortalities of squirrels)

(Installing official squirrel feeding stations around campus)

Question 5) which management strategies would you **oppose**? (check all that apply)

(Placing rodent poisons around campus)

(Trapping squirrels and sedate and euthanasia them)

(Trapping a portion of the squirrels and transferring them to Lick Creek Park)

(Increasing the number of nest boxes on campus)

(Installing squirrel crossing sign in an attempt to reduce road mortalities of squirrels)

(Installing official squirrel feeding stations around campus)

(None of the above)

Question 6) if the student body was informed that strategies you did not prefer or that you were opposed to were implemented in November 2005 would you respond in any way?

(yes, no)

Question 7) What would your response be to the implementation of strategies you opposed?

(open-ended)

Question 8) Imagine if you were to respond to a squirrel management strategy that you opposed. How would the people who are most important to you view your response listed in question 7?

(very negatively – very positively)

Question 9) Again imagine if you were to respond to a squirrel management strategy that you opposed. Describe the reaction to your response in question 7 from the people who are most important to you.

(strongly discourage – strongly encourage)

Question 10) Which management strategies if any would you support? (check all that apply)

(Placing rodent poisons around campus)

(Trapping squirrels and sedate and euthanasia them)

(Trapping a portion of the squirrels and transferring them to Lick Creek Park)

(Increasing the number of nest boxes on campus)

(Installing squirrel crossing sign in an attempt to reduce road mortalities of squirrels)

(Installing official squirrel feeding stations around campus)

(None of the above)

Question 11) if the student body was informed that strategies you preferred or supported were implemented would you in any way respond?

(yes, no)

Question 12) what would your response be to the implementation of strategies you support?

(open-ended)

Question 13) Imagine if you were to respond to a squirrel management strategy that you supported how would the people who are most important to you view your response listed in question 12?

(very negatively – very positively)

Question 14) Describe the support for your response listed in question 12 from the people who are most important to you.

(strongly discourage – strongly encourage)

Question 15) If you were talking to someone you did not know, what number on the following scale (0 to 10) would described your understanding and knowledge of fox squirrels.

(0 – 10)

Question 16) Please check all of the management strategies used to manage wildlife that you are familiar with.

(Placing rodent poisons around campus)

(Trapping squirrels and sedate and euthanasia them)

(Trapping a portion of the squirrels and transferring them to Lick Creek Park)

(Increasing the number of nest boxes on campus)

(Installing squirrel crossing sign in an attempt to reduce road mortalities of squirrels)

(Installing official squirrel feeding stations around campus)

(None of the above)

Question 17) Please check all of the management strategies used to manage wildlife that you have personally been involved with.

(Placing rodent poisons around campus)

(Trapping squirrels and sedate and euthanasia them)

(Trapping a portion of the squirrels and transferring them to Lick Creek Park)

(Increasing the number of nest boxes on campus)

(Installing squirrel crossing sign in an attempt to reduce road mortalities of squirrels)

(Installing official squirrel feeding stations around campus)

(None of the above)

Question 18) Within the last 12 months about how many times have you talked about squirrels?

(none)

(0 – 5)

(6 – 10)

(11 – 15)

(more than 15)

Question 19) Within the last 12 months about how many times have you talked about the squirrels on the Texas A&M campus?

(none)

(0 – 5)

(6 – 10)

(11 – 15)

(more than 15)

Question 20) Briefly summarize your most recent conversation about squirrels

(open-ended)

Question 21) Please select any of the following civic behaviors you have undertaken in the last 12 months for any reason.

(Letter to editor)

(Attend a protest)

(Organize a public event)

(Letter to an official (elected or appointed))

(Signed a letter of protest)

(Criticized Texas A&M University administration)

(Voted in the United States presidential election of 2004)

(Attended meetings of nationally sanctioned organization)

(None of the above)

(Other public behaviors aimed at influencing policies)

Question 22) Please select any of the following civic behaviors you have undertaken in relation to wildlife or natural resources over the last 12 months.

(Letter to editor)

(Attend a protest)

(Organize a public event)

(Letter to an official (elected or appointed))

(Signed a letter of protest)

(Criticized Texas A&M University administration)

(Attended meetings of nationally sanctioned organization)

(None of the above)

(Other (please specify))

Question 23) Please check any of the following organizations you are involved with

(Society for conservation biology)

(Wildlife society)

(Environmental Issues Committee)

(Aggies Cleaning the Environment)

(Texas Environmental Action Coalition)

(Aggie Feral Cat Alliance of Texas)

(Soil and Water Conservation Society)

(National Association of Environmental Professionals)

(Others (please specify any addition organizations active on Campus or in the Bryan/College Station community that you are a member))

Questions 24) Last week how many hours did you spend on activities related to the organization listed in question 23?

None

1 – 2

2 – 4

Greater than 4

Question 25) Using the scale provided evaluate the following behaviors

1-Very positively

2-Generally positively

3-Mixed: about equal positively as negatively

4-Generally negatively

5-Very negatively

(Writing a Letter to the editor)

(Attending a protest)

(Organizing a public event)

(Writing a letter to an official (elected or appointed) to express your opinion)

(Calling an official (elected or appointed) to express your opinion)

(Signed a letter of petition)

(Verbally criticized administrators or official)

(Attended meetings of organization attempting to change decisions, laws, or)
(regulation they disagree with)

(Expressing your opinion about public decision to friends or family)

Question 26) Are you Male or Female?

(male, female)

Question 27) What was your age on your last birthday?

(number)

Question 28) What is your current occupation?

(undergraduate student)

(graduate student)

(faculty or staff)

(other)

Please add any additional comment here

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