FERAL CAT VIRUS INFECTION PREVALENCE, SURVIVAL, POPULATION DENSITY, AND MULTI-SCALE HABITAT USE IN AN EXURBAN LANDSCAPE

By

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Abstract

Domestic cats (*Felis catus*) are ubiquitous in natural and anthropogenically-modified ecosystems and they negatively impact their environments. Prior research into feral cat ecology in the U.S. has focused primarily on feline leukemia virus (FeLV) and feline immunodeficiency virus (FIV) prevalence, spatial organization, and home ranges of cats in urban and rural areas, but information concerning habitat use or exurban feral cat populations is sparse. The purpose of my research is to investigate feral cat virus infection prevalence; survival; population density; and macro- and microhabitat use in exurban Russellville, Arkansas. During October 2012 – August 2013, I captured 93 feral cats and collected blood from each individual for FeLV/FIV testing. I also fit mortality-sensing radiocollars on 29 adult cats and conducted radiotelemetry over 65 weeks to determine survival, home range sizes, and to identify summer daytime resting sites (DRSs). I used multivariate analyses to determine 2nd, 3rd, and 4th order habitat use. The combined FeLV and FIV prevalence was 29.02% and I estimated annual feral cat survival as 0.99 with male cats having a greater survival rate than females. In general, annual home range areas (15.17 – 19.76ha) were larger than warm season (9.03 – 15.33ha), but not different from cold season ranges (11.09 – 23.91ha). Home ranges were larger than core areas (2.97 – 5.09ha) for all seasons. Male cat home ranges (22.14 – 29.17ha) were larger than female ranges (9.60 – 12.26ha), but virus status and body condition score did not influence range sizes. Feral cat population density within Russellville was 0.10cats/ha. Second and 3rd order habitat use analyses indicated feral cats used open-low and medium-high intensity development disproportionately to land cover availability and 4th order analysis identified thick vegetation within these land...
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*Keywords:* Felis catus, Feral Cat, Exurban, Feline Leukemia Virus, Feline Immunodeficiency Virus, Population Density, Home Range, Macrohabitat, Microhabitat, Daytime Resting Sites
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THESIS INTRODUCTION

Domestic cats (*Felis catus*) have been introduced worldwide (United States: Guttilla and Stapp 2010, Horn et al. 2011; Europe: Devillard et al. 2003, Bonanni et al. 2007; Australia: Jones and Coman 1982, Edwards et al. 2001; New Zealand: Norbury et al. 1998, Harper 2007; and Africa: Tennent and Downs 2008) and have proven to be a highly adaptive species as they have established feral populations in a variety of habitats (Devillard et al. 2003, Tennent and Downs 2008, Longcore et al. 2009, Loyd and Miller 2010). Outdoor cats are generally categorized based on their confinement status, level of dependence on humans, and/or degree of socialization (Clarke and Pacin 2002, Levy et al. 2002, Levy and Crawford 2004, Baker at al. 2005). Nonetheless, a cat’s status as feral, stray, or free-roaming is imprecise and can fluctuate from one category to another over time (Clarke and Pacin 2002, Levy et al. 2002, Levy and Crawford 2004). For instance, the term feral typically applies to cats born in the wild that are untamed and elusive, living independent of humans (Levy and Crawford 2004, Baker et al. 2005). However, some feral cats are subsidized by human refuse or doorstep food, but maintain their untamed behavior (Clarke and Pacin 2002). The term stray typically refers to homeless cats that were abandoned or lost, yet exhibit varying degrees of tameness and dependence on humans for food or shelter (Pearre et al. 1998, Clarke and Pacin 2002, Levy et al. 2002, Baker et al. 2005). Feeding stray cats is a common practice and many people are protective of the cats they care for (Levy et al. 2002); thus, a stray cat can easily become a loosely-owned free-roaming cat. The term free-roaming is used to identify any cat not confined to a yard or house, whether it is stray, feral, or an owned pet spending all or part of its time outdoors (Clarke and Pacin 2002, Levy and Crawford...
Feral cats are ubiquitous in natural and anthropogenically-modified ecosystems where they can negatively impact their communities. Yet, estimates of feral, stray, or free-roaming cats in the United States vary widely: 10 – 50 million (Schmidt et al. 2007, Schmidt et al. 2009); 25 – 60 million (Lee et al. 2002); 60 – 100 million (Anderson et al. 2004, Jessup 2004, Levy and Crawford 2004, Loyd and Miller 2010); ≥100 million (Clarke and Pacin 2002). The impacts of feral cats on their communities include depredation on native wildlife; competition with native predators for prey (Ogan and Jurek 1997, Clarke and Pacin 2002, Schmidt et al. 2007, Schmidt et al. 2009, Guttilla and Stapp 2010); and potential for virus transmission to other wildlife species (Guttilla and Stapp 2010, Loyd and Miller 2010), domestic pets, and humans (Schmidt et al. 2009, Loyd and Miller 2010). Given these negative impacts on communities, feral cat populations are a concern of wildlife biologists and natural resource managers (Loyd and Miller 2010).

Most feral cat research in the United States has been conducted in rural (New Kent County, VA: Mitchell and Beck 1992; Randolph County, NC: Nutter et al. 2004) or urban and suburban areas (Brooklyn, NY: Calhoon and Haspel 1989; Henrico County, VA: Mitchell and Beck 1992; Raleigh, NC and Gainesville, FL: Lee et al. 2002; Randolph County, NC: Nutter et al. 2004; Caldwell, TX: Schmidt et al. 2007, Schmidt et al. 2009; Champaign and Urbana, IL: Horn et al. 2011), and information regarding exurban feral cats is scant. There is no decisive definition for exurban (Ban and Ahlqvist 2009, Walter 2011), but it is typically characterized as having relatively low-housing density in a heterogeneous landscape, combining natural and anthropogenic features, and
existing within a matrix of natural landscapes such as state and national parks and conservation areas (Theobold 2004, Hansen et al. 2005). Native species tend to concentrate in these natural areas, thus exurban development may have greater impact on natural communities than other types of development (Hansen et al. 2005).

Exurban development is the fastest growing land-use form in the United States, covering 5 – 10 times more land area than urban and suburban areas in the year 2000 and increasing at a rate of 10 – 15% per year (Theobald 2004). The effects of exurban development on wildlife and biodiversity are just beginning to be understood, but reduced survival and reproduction of native species and increased exotic species are associated with increasing housing density (Odell and Knight 2001, Hansen et al. 2005). Levy and Crawford (2004) reviewed studies about the number of feral cats fed by residents in Alachua County, FL, Santa Clara County, CA, San Diego County, CA, and 4 towns in MA and concluded that 0.5 feral cats/household was a reasonable estimate of a community’s feral cat population. Therefore, the number of feral cats in an area is likely to be positively correlated with increasing housing developments. The ability of feral cats to exploit different habitats and prey sources may exacerbate the impacts of exurban development on surrounding natural communities.

The goal of my study was to investigate feral cat ecology in an exurban area to better understand the potential impacts of feral cats within the populous areas of the city and its surrounding natural communities. Feral cats infected with feline leukemia (FeLV) or feline immunodeficiency virus (FIV) have the potential to transmit these viruses to outdoor pet cats or other feral cats and FeLV may be transmitted to Arkansas’ native wild felids: the bobcat (Lynx rufus) and mountain lion (Puma concolor; Schmidt et al. 2009,
Loyd and Miller 2010). Survival of feral cats also influences the potential impacts cats have on their communities over time and may be influenced by virus infection status, sex, and habitat type. Therefore, my specific objectives in Chapter 1 were to quantify FeLV and FIV prevalence in a feral cat population and to examine survival of adult feral cats in an exurban area.

Understanding how feral cats use habitats is essential for evaluating environmental impacts of cat populations (Johnson 1980) and for effective feral cat management. High-density feral cat populations may have a greater influence on their communities than low-density populations (Levy and Crawford 2004). For example, the rates of virus transmission may be greater in populations with high-density feral cat populations because the frequency of contact among individual cats is likely greater compared to low-density populations (Fromont et al. 2003). Home range areas and spatial use can provide insight into the influence of cats on their communities and help managers to focus trapping effort. In Chapter 2, I examined the structure of an exurban feral cat population in terms of density and space use. Specifically, my objectives were to estimate population density and quantify annual and seasonal home range areas of feral cats in an exurban landscape. I also compared the habitat composition within the home ranges and habitats available within the study area (2nd order use) and habitat composition of the core areas with habitats available in the home ranges (3rd order use; Johnson 1980).

Microhabitat requirements and use by feral cats is poorly studied despite the importance of shelter to cat survival (Calhoon and Haspel 1989, Harper 2007, Horn et al. 2011). Feral cats are mostly nocturnal and seek daytime resting sites (DRSs) that provide
protection from weather and predators (Jones and Coman 1982, Barratt 1997, Norbury et al. 1998). There is no published information regarding characteristics of daytime resting sites (DRSs) used by feral cats in the United States, so in Chapter 3 I examined summer DRS use by feral cats via microhabitat and macrohabitat analyses.

**LITERATURE CITED**


CHAPTER 1:

VIRUS INFECTION PREVALENCE AND SURVIVAL OF FERAL CATS IN AN EXURBAN CITY

Feral cats have the potential to carry and transmit viruses and parasites to domestic pets, humans, and other wildlife (Mitchell and Beck 1992, Genovesi et al. 1995, Ogan and Jurek 1997, Lepczyk et al. 2003, Anderson et al. 2004, Levy and Crawford 2004, Nutter et al. 2004, Foley et al. 2005, Schmidt et al. 2007, Schmidt et al. 2009, Loyd and Miller 2010). The most common infectious diseases of cats are FIV and FeLV, both of which cause immunosuppression in cats and occur worldwide (Lee et al. 2002, Little 2005). Transmission of FIV is highly associated with territorial fighting behaviors of intact male cats (Lee et al. 2005), but also has potential for venereal transmission (Little 2005). The major modes of FeLV transmission are grooming behavior (Fromont et al. 1997), milk, blood, and urine; kittens are more susceptible to FeLV infections than adults (Lee et al. 2005). Transmission of FIV from one species to another is rare; however, FeLV has been identified in populations of the endangered Florida panther (*Puma concolor coryi*) and the critically endangered Iberian lynx (*Lynx pardinus*; O’Brien et al. 2012). It is unknown how these felids first contracted FeLV, but contact with or consumption of an infected domestic cat are the leading hypotheses (Clarke and Pacin 2002).

Epidemiologic studies conducted in Florida and North Carolina estimated FIV and FeLV prevalence in feral cats at 3.5% and 4.3%, respectively (Lee et al. 2002), but infection rates vary regionally (Table 1.1; Little 2005). For instance, feral populations may have similar infection rates for both viruses or one virus may be disproportionately
more prevalent than the other in the same population. Within the same area, infection rates can vary widely between categories (i.e., feral, stray, and free-roaming) of populations or among populations of the same category.

The only study to examine FeLV and FIV patterns across the USA occurred through 2000 – 2011 (Chhetri et al. 2013). Chhetri et al. (2013) obtained 47,125 positive IDEXX SNAP FIV/FeLV Combo test results from various veterinary practices, IDEXX reference laboratories, and IDEXX-sponsored prevalence studies from across the contiguous USA. They did not have precise information on the category (i.e., feral, stray, free-roaming pet or indoor pet) of the cats tested. They calculated the proportional morbidity ratio (PMR; [FIV/FeLV]) and constructed a choropleth map of PMRs by state to identify infection patterns across the country. Infections of FeLV occurred more frequently than FIV (PMR <0.67) in the western USA, whereas FIV infections occurred more frequently than FeLV (PMR >1) in the southern and eastern portions of the USA.

Survival rates among adult feral cats are difficult to quantify because of undetected deaths, dispersal from study areas, and removal by humans (Baker et al. 2010). For instance, a 42-month study of feral cats (n = 39) in inner-city Berlin reported 9 disappearances, 15 deaths, and 4 adoptions, with only a 33% survival rate (Kalz et al. 2000). A county-wide study in north central Florida surveyed 101 caretakers of 132 trap-neuter-release colonies containing 920 unowned cats, of which 149 cats disappeared, 151 died, and 238 were adopted during a 9-month period (Centonze and Levy 2002). Semi-feral cats whose diets are subsidized by human feeding appear to have higher survival rates than feral cats (Schmidt et al. 2007). Schmidt et al. (2007) monitored feral (n = 29) and semi-feral (cats directly fed by a resident; n = 14) cats in a suburban area of Texas
and calculated 14-month survival at 56% and 90%, respectively. Horn et al. (2011) examined 27 unowned cats in Champaign-Urbana, Illinois and determined that only 50% of unowned cats would be expected to survive >392 days. No telemetry study has estimated the life span of adult feral cats, but anecdotal reports estimate 2 – 3 years (Anderson et al. 2004).

Survival of feral cats infected with FIV or FeLV is understudied, but is important for understanding virus transmission within and among populations. A study by Mari et al. (2004) found that pet cats infected with FeLV were asymptomatic for 80 – 300 days before developing clinical symptoms of the disease, after which approximately 80% died <2.5 – 3.5 years. Hofmann-Lehmann et al. (1997) estimated the asymptomatic phase lasted approximately 3.5 years in pet cats infected with FIV and biochemical parameters of infected cats and control groups were not statistically different until 9 months after infection. They also reported that all 15 cats experimentally infected with FIV and housed in hygienic conditions were alive at the end of their 6.5-year study. Considering that feral cats infected with FeLV or FIV may survive for several years before and after developing clinical signs of the disease, there are likely ample opportunities for virus transmission within outdoor populations. Also, the number of disappearances reported in survival studies suggests that many cats disperse from their regular territories, thus increasing the potential for virus transmission among feral populations. In addition, wildlife biologists and natural resource managers cannot determine the health status of feral cats by physical appearance alone because seemingly healthy cats may be in the asymptomatic phase of disease (Hofmann-Lehmann et al. 1997).
Understanding feral cat virus infection prevalence and survival is essential for identifying the potential impacts feral cats have on their communities and for effective cat management. Given that infection rates vary regionally (Little 2005), prevalence research should occur at the local scale in order to determine the need for feral cat management and enact management that will effectively reduce infection prevalence in feral cat populations. To my knowledge, only 1 study has examined infection prevalence of feral cats in Arkansas and neighboring states (Chhetri et al. 2013), but no one has examined these viruses specifically in an exurban area. Therefore, my goal was to quantify FeLV and FIV prevalence and survival of feral cats in an exurban city in Arkansas.

METHODS

Study Area

Russellville is a growing exurban city in central northwest Arkansas, located in the Arkansas River Valley between the Ouachita and Ozark National Forests. The nearest urban cities to Russellville with populations >50,000 are Conway (2013 population 63,816) located 75 km to the southeast, Little Rock (2013 population 197,357) located 97 km to the southeast, and Fort Smith (2013 population 87,650) located 135 km to the west (United States Census Bureau 2014). In 2012, the estimated population of Russellville was 28,533 people (389 people/km²; United States Census Bureau 2014). Between 2000 and 2010, Russellville’s population increased 18.9% from 23,682 people (323 people/km²) to 27,920 people (381 people/km²; United States Census Bureau 2000). However, the number of housing units increased by only 8.7% from 10,234 in 2000 (1340 houses/km²; United States Census Bureau 2000) to 11,124 in 2010 (152
During this study, Russellville covered 73 km$^2$ and 46% consisted of developed land: 8.05 km$^2$ (11%) developed open spaces with <20% impervious surfaces; 16.92 km$^2$ (23%) low-intensity developments with 20 – 49% impervious surfaces; 6.69 km$^2$ (9%) medium-intensity developments with 50 – 79% impervious surfaces; and 2.52 km$^2$ (3%) high-intensity developments with >80% impervious surfaces (Jin et al. 2013). Forests covered 31% of Russellville: 16.64 km$^2$ (23%) evergreen; 4.68 km$^2$ (6%) deciduous; and 1.52 km$^2$ (2%) mixed evergreen and deciduous. Pasture and hay fields comprised 13.71 km$^2$ (19%). The remaining land covers (4%) in Russellville, grassland/shrub/scrub; open water; wetlands; cultivated crops; and barren rock, each comprised ≤1%. Road density in Russellville was 6.83 km/km$^2$ (total length = 500 km) and railroad density was 0.32 km/km$^2$ (total length = 23.60 km).

During the study, Russellville’s mean monthly temperature for the cold seasons (November – March) was 7.65 ± 3.99°C (monthly mean ± SD for all weather-related numbers) and the coldest month was December 2013 (monthly mean = 4.44°C; Weather Underground 2014). The mean monthly temperature for the warm season (April – October) was 22.46 ± 4.78°C and the warmest month was August 2013 (monthly mean = 27.22°C; Weather Underground 2014). Mean monthly precipitation during the 15-month study was 7.98 ± 4.06 cm and did not differ between the cold and warm seasons ($t_{14} = 0.70 \ P = 0.249$; PROC TTEST, $\alpha = 0.05$ for all statistical analyses; SAS Institute, Cary, North Carolina).

Because Russellville is an exurban city comprised of populous urban areas intermixed with relatively natural areas, I attempted to sample cats from the range of
habitats available within the city. I placed traps in 38 locations that included 23 populous urban areas and 15 relatively natural areas (Figure 1.1). I determined trapping locations based on the land owner or manager granting permission to trap cats on their property. The urban locations included 3 apartment complexes, 2 grocery stores, 3 fast food restaurants, 1 diner, 7 businesses, 2 city parks, 3 residences, and the Arkansas Tech University campus and physical plant. The natural areas include 7 city parks, 1 state park, 2 parks managed by the Army Corps of Engineers, 3 residences, and 2 businesses. However, 2 locations grouped with natural habitats were closely bordered by urban areas.

**Capture and Animal Handling**

I conducted trapping and handling activities in accordance with the guidelines of the American Society of Mammalogists (Sikes and Gannon 2011) to ensure the ethical treatment and safety of all captured animals. During October 2012 – August 2013, I set ≤25 custom-made live-cage traps (30x30x70cm) 2 – 5 nights per week between 1700 – 2030 hr. I checked and retrieved traps the following mornings between 0600 – 1030 hr. Trap effort was high (i.e., 125 trap nights/week) through December 2012 when the last of 24 radiocollars were initially deployed, then trap effort decreased until I had collected blood samples from 90 different cats. I used commercial canned cat food as bait and camouflaged traps within vegetated areas (i.e., bushes, tall grass, and low hanging tree branches) of 1 – 5 trapping locations per night. Patchy vegetation at the trapping locations prohibited trapping along transects and using standardized trap spacing.

I immediately released all captured non-target animals (e.g., raccoon *Procyon lotor*, opossum *Didelphis virginiana*, skunk *Mephitis mephitis*) and all cats wearing collars because they were likely owned free-roaming cats. I also used a remote
microchip reader (Biomark model 604, Biomark, Boise, Idaho) to scan for passive integrated transponder (PIT) tags. If a PIT tag was present, I presumed the cat was owned and released it immediately. I considered all cats without PIT tags or collars to be unowned (Horn et al. 2011) and feral. I did not distinguish between semi-feral (unowned cats that were directly fed by a resident) and feral cats (cats not directly fed; Schmidt et al. 2007) because some cats were feral at the time when radiocollared and became semi-feral during the course of the study.

I estimated weight and anesthetized feral cats in situ via intramuscular injection of approximately 0.04 mg/kg of dexmedetomidine HCL (Dexdomitor; Orion Corporation, Espoo, Finland; Granholm et al. 2006) and used an intramuscular injection of 0.04 mg/kg antagonist atipamezole HCL to reverse sedation (Antisedan; Orion Corporation; Granholm et al. 2006). If a feral cat appeared especially excited or resilient to sedation, a higher dose ≤0.10 mg/kg of each drug was required (Horn et al. 2011). I weighed, sexed, and examined all cats for neuter scars. I assigned each cat a body condition score (BCS) from 1 (emaciated) to 9 (grossly obese), with a score of 5 being ideal based on palpability of ribs and spine, definition of waist, and presence or absence of abdominal fat pad (Nestle Purina Pet Care Center, Scott et al. 2002). In addition, I collected 0.1 – 0.3 mL of blood for FeLV/FIV testing (SNAP FIV/FeLV Combo Test, Idexx Laboratories) in the laboratory. I aged kittens based by on physical development: eyes open 7 – 10 days; eruption of milk teeth begins on approximately day 12 and continues until week 5; walking occurs at 3 weeks, but is not steady until week 4; eruption of adult incisors around week 14 (Bateson 2000). If I captured ≥2 kittens that were ≤14 weeks old in the same trap, I assumed they were littermates that had similar exposure to viruses. In this
situation, I combined their blood and ran a single FIV/FeLV test for the litter which is a common practice in veterinary clinics for FIV/FeLV screening of litters (M. Lombardi DVM, United States Fish and Wildlife Service, personal communication). If the test was positive, I would have no way of knowing if 1 or all kittens were positive and therefore counted the litter as 1 individual. However, if the test was negative, I included each kitten in the litter as 1 negative result. I implanted a 9-mm 134.2 kHz PIT tag (Biomark HPT, Biomark, Boise, Idaho) subcutaneously to mark each feral cat for identification if recaptured and fit mortality-sensing radiocollars (38 g, 150-152 MHz; Advanced Telemetry Systems [ATS], Isanti, Minnesota) on a subset of adult cats (n = 31). I only radiocollared adult cats weighing ≥1.3 kg to ensure the radiocollar weight did not exceed 3% of the body mass of the cat (Schmidt et al. 2007, Horn et al. 2011). I released all healthy feral cats at the capture site after they recovered from sedation, but I took cats that were in extremely poor condition (BSC <2 and apparently suffering) to Russellville Animal Control for euthanasia.

**Virus Infection Prevalence**

I refrigerated (1 – 4 °C) blood samples from captured cats in microtainer plasma separator tubes with lithium heparin (Becton, Dickinson, and Company, Franklin Lakes, New Jersey) for ≤2 months. I centrifuged blood samples to separate the plasma, which I then used to conduct SNAP FIV/FeLV Combo Tests (Idexx Laboratories Inc., Westbrook, Maine). I performed tests per Idexx instructions and recorded results only for tests that showed positive control indicators.

I identified trends in virus infection prevalence between sexes, BCS, and habitat of capture location (i.e., natural vs. urban) for the captured feral cats. I calculated
infection prevalence as a proportion of captured cats that tested positive for FeLV and/or FIV and ran G-tests (PROC FREQ, α = 0.05 for all statistical analyses; SAS Institute, Cary, North Carolina) to determine if virus infection status was independent of sex, BCS, and habitat at capture location.

Within Arkansas, Chhetri et al. (2013) collected 18 positive IDEXX SNAP tests (FIV = 10, FeLV = 18) from 12 counties, but no tests were from Pope County where Russellville is located (IDEXX 2011). They also found that Arkansas PMRs (no. FIV positive tests / no. FeLV positive tests) ranged 0.48 – 0.67, but all surrounding states had PMRs ranging 0.67 – 2.05 and a spatial scan test included Arkansas in a cluster of states where FIV infections are greater than FeLV among cats (Chhetri et al. 2013). I calculated PMR within Russellville to compare against the PMR for Arkansas and surrounding states in Chhetri et al. (2013). I also calculated the PMR for male and female cats in this study.

Lastly, I created a shapefile in ArcGIS (Environmental Systems Research Institute, Redlands, California) that contained the virus infection status and capture location of all tested cats to identify the proportion of infected animals at a given location. Within ArcMap, I overlayed this shapefile over a map of Russellville and examined the potential for virus hotspots by using Geospatial Modeling Environment (GME; Beyer 2012) to identify a 50% kernel density estimate (ISOPLETH command [quantile = 0.50]) of infected cats throughout the city. I used GME (COMMAND ISECTPOLYRST) and ArcMap to identify the land cover composition within the virus hotspot and then ran a G-test (PROC FREQ) to identify if it differed from the land cover available in Russellville.
Survival

I used an R410 receiver (ATS), a hand-held 3-element Yagi antenna (ATS), and ground-based radiotelemetry techniques to track all radiocollared cats and determine their survival from October 2012 – December 2013. I began monitoring survival of feral cats <4 days of collar deployment by listening for a signal on each cat 2 – 3 times per week. If a radiocollar exhibited a mortality signal, I immediately collected the cat and identified the cause of mortality. A licensed veterinarian performed a necropsy on each deceased cat to confirm cause of death, age, and reproductive status. I classified cause of mortality into 4 categories: predation; disease; vehicle collision; and unknown (Urbanek et al. 2009).

I calculated both the naïve annual survival estimate (\(\frac{[1 – (\text{no. mortalities}/(\text{total no. cats tracked} – \text{no. censored}))]/ \text{no. weeks tracked}}{52}\)) and I used the staggered entry and the known-fate survival estimator in Program MARK (Colorado State University, Fort Collins, Colorado) to estimate the maximum likelihood annual survival of feral cats. If a cat disappeared from the study area, it was recorded as a censored observation (Brasher et al. 2006, Horn et al. 2011, Cooch and White 2012). The factors likely to influence survival of feral cats are sex, infection status, BCS, season, and whether the cat’s home range is located in an urban or natural area (Table 1.2). Therefore, I developed 12 a priori models based on these factors and used Akaike Information Criterion adjusted for small sample size (AIC<sub>c</sub>) to determine their effects on feral cat survival (Table 1.3).

The model set included models with single variables that may have an effect on the survival of feral cats (Table 1.3). Male feral cats tend to have larger home ranges...
than females (Jones and Coman 1982, Harper 2007, Schmidt et al. 2007, Guttilla and Stapp 2010, Horn et al. 2011), which may increase risk exposure of males as they traverse their regular territories. Feral cats infected with FIV or FeLV or cats in poor body condition (BCS <5) are likely unhealthy or physically weak. Consequently, these individuals may have lower survival than cats that tested negative for FIV/FeLV and cats with BCS ≥5. Summer in Russellville is hot and dry, so few ditches hold water year round. Therefore, feral cats may have difficulty obtaining water during the warm season and experience reduced survival compared to the cold season. Urban feral cats have more reliable food resources, which may reduce mortality risks associated with foraging effort compared to cats in more natural areas of an exurban landscape.

I also included models with combinations of variables that may have synergistic effects on feral cat survival in the model set (Table 1.3). Female feral cats may have higher survival during the warm season because they will likely spend less time traversing their home ranges with their young; thus, this behavior may potentially reduce their exposure to mortality risks compared to male cats. Urban cats have more stable food sources than cats residing mostly in natural areas, a condition that may be more pronounced during winter. Thus, the reduced foraging effort and exposure to risks may increase survival of urban cats compared to cats in natural areas during the cold season. In addition, urban feral cats typically form colonies around concentrated food sources whereas rural cats are usually solitary (Liberg et al. 2000); hence, male cats in natural areas may need to travel farther than urban males to find mates, likely increasing exposure to mortality risks and reducing their survival. Consequently, urban female cats may have higher survival during the cold season than urban males or both sexes in
Cats infected with FeLV or FIV with a BCS <5 may indicate later stages of infection and may experience higher mortality from illness than infected individuals with BCS ≥5. Therefore, cats that tested positive for FeLV or FIV and that had a BCS >5 may have higher survival than infected cats with low BCSs.

I considered only models ≤2 ΔAICc values from the most parsimonious model (Burnham and Anderson 2004, Cooch and White 2012) and with AICc values less than the model holding survival constant as supported (Burnham and Anderson 2004, Cooch and White 2012). Model deviance; AICc relative importance weights; unstandardized parameter estimates and standard error; and signs of overdispersion were examined for supporting evidence that a variable affected survival. Known-fate models in Program MARK are considered saturated and thought to fit the data perfectly. Thus, there is no goodness of fit test for known-fate data (Brasher et al. 2006, Urbanek et al. 2009, Cooch and White 2012). Consequently, I examined for potential overdispersion by adjusting the variance inflation factor (ê) in increments of 0.25 from 1 (model fits the data) to 3 (model is overdispersed) and examined changes in model ranks (Brasher et al. 2006, Urbanek et al. 2009).

RESULTS

I set 2,307 traps (1,149 in natural areas and 1,158 in urban areas) and had a total of 2,120 effective trap nights: 112 traps were tripped but empty; 140 non-target animals were captured; and 122 cats were trapped. Twenty-one of the captured cats were recaptures. Of the 101 unique cats captured, 1 was a pet and 7 escaped before processing, so I collected data from 93 feral cats (64 males and 29 females). Most of the cats sampled were adults (n = 75; 52 males and 23 females), but I also sampled 18
immature cats <6 months old (12 males and 6 females). I had greater trapping success at urban sites (n = 68; 49 males and 19 females; 58 adults and 10 juveniles) than natural sites (n = 25; 15 males and 10 females; 17 adults and 8 juveniles) although I visually detected several cats at the natural sites. Overall catch per unit effort was 1 unique cat/25 trap nights, but catch per unit effort was 3 times lower in natural areas (1 cat/50 trap nights) than urban areas (1 cat/16.7 trap nights).

The majority of the cats sampled (n = 58) were in ideal body condition (BCS = 5), 22 cats were underweight (BCSs between 2 – 4) and 13 were overweight (BCSs of 6 or 7). Sample sizes of cats for each BCS, particularly the lower and upper ranges, were too small to run valid statistical analyses, so I grouped cats by body condition (underweight: BCS ≤4, ideal: BCS = 5, overweight: BCS ≥6). Body condition did not differ by sex (G₂ = 4.57 P = 0.102) or age (G₂ = 2.21 P = 0.331). However, I trapped more underweight and less ideal weight cats than expected at natural sites, and more ideal weight cats than expected at urban sites (G₂ = 7.38 P = 0.025). One captured cat was transported to Russellville Animal Control for euthanasia because he was in poor condition (BCS = 2) and had bleeding tumors on the pads of all 4 feet.

**Virus Infection Prevalence**

I ran 90 FeLV/FIV SNAP tests; however, 1 test was discarded because it was run incorrectly and 2 tests contained the combined blood from litters of kittens <14 weeks old (a litter of 2 and a litter of 4). Both litters tested negative, so I counted each kitten as an individual instead of the litter as a whole, which resulted in 93 total cats tested. Overall infection prevalence was 29.02% (15.05% FeLV positive, 11.82% FIV positive, and 2.15% positive for both FeLV and FIV). Sample sizes for cats that were positive for
FeLV, FIV, or FeLV/FIV were too small for valid statistical analyses, so I grouped cats by infected or uninfected status to examine prevalence. Infection prevalence (Figure 1.2) did not differ by sex \((G_1 = 1.48 \, P = 0.224)\), habitat at capture location \((G_1 = 0.02 \, P = 0.894)\), or body condition \((G_2 = 1.06 \, P = 0.588)\). Calculated PMR of feral cats in Russellville was 0.81. Female feral cats had a lower PMR (0.20) than male cats (1.09).

Infection prevalence of FeLV and/or FIV ranged from 0% – 100% at any given trapping location, however the 2 locations with 100% prevalence had sample sizes of 1 cat. Of the locations with >1 feral cat tested, I identified 3 locations with 66.67% infection prevalence: 2 natural locations in northern Russellville and 1 urban location in southeast Russellville. The virus hotspot was 974.6ha (13.31% of Russellville) and encompassed the northern part of the city, south through central Russellville, and into the southeast quadrant of the city (Figure 1.4). The land cover composition within the hotspot area was mostly open-low intensity development (51.43%), followed by medium-high intensity development (23.22%), pasture and hay fields (14.37%), forests (8.61%), other (1.32%), and open water (1.05%). Relative to the land cover within Russellville, the virus hotspot included open-low and medium-high intensity developed areas more than expected and forests less than expected \((G_5 = 21.58 \, P < 0.001)\).

**Survival**

Of the 31 adult feral cats radiocollared, I tracked 29 cats (13 males and 16 females; 10 infected with FELV and/or FIV and 19 uninfected; 22 cats caught in urban areas and 7 cats captured in natural areas; BCS median 5 (range 2,7) for 3 – 57 weeks \((41.83 \pm 0.58SE)\). Two radiocollars were apparently fit on owned cats and were removed by their owners <1 day of collar deployment and 19 cats were censored during the course
of the study. In addition, I recorded 4 mortalities: 1 vehicle collision, 1 disease (probable bacterial pneumonia [Streptococcus pneumoniae]), and 2 from unknown causes. All cats that died during the study were female; 2 occupied urban areas and 2 were from natural areas; 3 were in ideal body condition at the time of capture (BCS = 5) and 1 was slightly underweight (BCS = 4). Both cats that died of unknown causes tested positive for FeLV whereas the other 2 cats tested negative for both FeLV and FIV. The female that died from probable bacterial pneumonia was pregnant with 4 kittens and approximately 10 days from parturition. The naïve annual survival estimate for cats in this study was 0.73.

Of the 12 a priori models, I identified 3 competing models that included 61% of the Akaike model weight (Table 1.3). Feral cat survival was influenced the most by the sex of the cats and this variable was included in all competing models (relative Akaike weight $\omega = 0.61$). Given that only female feral cats experienced known mortalities during the study, these results indicated that male feral cats have higher rates of survival than female feral cats. The remaining variables in the competing models included habitat of capture location ($\omega = 0.18$) and season in which mortality occurred ($\omega = 0.12$). These models indicated that feral cats captured in urban locations had higher survival rates than cats captured in natural locations and that feral cats experienced higher survival rates in the cold season compared to the warm season. The models containing habitat and season had lower deviance than the model considering only the sex of the cats which provided some evidence that these parameters may contribute to annual survival rates in addition to the variable for sex. Conversely, the regression coefficients for both the habitat and season parameters had less influence within the models than did the sex of the cats. Moreover, unlike the 95% confidence intervals for the coefficient of the sex parameter (-
16.62 – 17.85), the confidence intervals for the coefficients of both habitat (-0.98 – 2.95) and season (-1.71 – 2.22) overlapped 0, indicating non-significance. Adjusting č changed rank order of the models suggesting overdispersion of the data and that the models containing habitat of capture location and season of mortality were unsupported. The top model remained stable through ĉ = 2.25 and thus the sex of the cats was the only contributing factor to survival in this study; the estimated annual survival from this model was 0.99.

**DISCUSSION**

Given that FeLV and FIV prevalence can vary across regions and that survival of feral cats influences potential impacts these cats have within their communities, my objectives were to quantify FeLV and FIV prevalence and survival of adult feral cats within an exurban city. I detected higher prevalence of FeLV than FIV and found an overall infection prevalence of nearly 30%. The virus hotspot comprised 1/7th of the area within the city and most of the hotspot occupied open-low and medium-high intensity developed land cover. Despite the relatively high infection prevalence, annual survival of adult feral cats in Russellville was high and male feral cats appeared to have a higher rate of survival than female cats. Feral cats infected with FeLV or FIV pose health risks to free-roaming pet cats and other wild felids and the high survival rates of the infected cats monitored in this study suggests ample opportunities for transmission of these viruses on a temporal scale. The combination of high infection prevalence and high survival rates among feral cats in Russellville indicates the need for feral cat management efforts in the city.
Virus Infection Prevalence

Lee et al. (2002) identified overall prevalence of FeLV at 4.3% and FIV at 3.5% among feral cats in Gainesville, FL and Raleigh, NC. Infection prevalence in Russellville was much higher and may exist as part of the regional variation reported in the literature (Lee et al. 2002, Little 2005, Natoli et al. 2005). However, the higher prevalence in my study may result from the lack of feral cat management in Russellville whereas in both Gainesville and Raleigh feral cats tested were part of an ongoing trap-neuter-release program. Given that FIV is most commonly transmitted between intact male cats during territorial disputes and a common mode of FeLV transmission is from mother to kittens (Lee et al. 2002), the act of neutering feral cats may reduce FeLV and FIV transmission within a population, but further research is warranted.

Lee et al. (2002) observed a higher prevalence of FeLV infection (5.3%) compared to FIV (2.3%) in NC, but not in FL (3.7% and 4.3%, respectively). In addition, they found male feral cats were more likely than female cats to test positive for FIV but not FeLV (Lee et al. 2002). In Russellville, I observed a slightly higher percentage of FeLV-positive tests than FIV-positive tests; however the combined FeLV and FIV prevalence between male and female feral cats was insignificant. The disadvantage of combining FeLV and FIV in my statistical analyses was the inability to detect the risk of FeLV or FIV infection between the sexes. However, calculating PMR for each sex enabled identification of higher frequency of FeLV infections relative to FIV infections in female cats and the inverse relationship in male cats, which is consistent with the disease-sex relationship identified in previous studies (Lee et al. 2002, Levy and Crawford 2004).
The calculated PMR in Russellville indicated a higher occurrence of FIV relative to FeLV infections compared to the estimated PMR for all of Arkansas (0.48 – 0.67; Chhetri et al. 2013). This discrepancy likely resulted from the different sampling techniques and target populations; Chhetri et al. (2013) did not distinguish among feral, stray, free-roaming pet cats, or indoor pet cats whereas I targeted feral cats specifically. Living outdoors has been identified as a predisposing factor for FeLV and FIV infection in pet cats (O’Conner et al. 1991, Lee et al. 2002). In O’Conner et al.’s (1991) study, free-roaming pets were 2.7 times as likely to test positive for FeLV and 4.8 times as likely to test positive for FIV compared to indoor cats. Therefore, it is reasonable to consider the cats in my study as a high-risk population because they were all living outdoors. In addition, Chhetri et al. (2013) collected 18 positive tests (FIV = 10, FeLV = 18) from 12 counties (results of only FIV from 2 counties, only FeLV from 7 counties, and both FeLV positive and FIV positive from 3 counties), but none from Pope County where Russellville is located (IDEXX 2011). Russellville’s PMR was within the range of PMRs that Chhetri et al. (2013) calculated for Oklahoma, Missouri, Tennessee, and Mississippi (0.67 – 1.10), but lower than PMRs in the remaining 2 bordering states, Texas and Louisiana (1.10 – 2.05).

The virus infection hotspot was a spatial cluster where half of the infected cats originated. Relative to the land cover within Russellville, the hotspot included disproportionately more open-low and medium-high intensity developed land. Epidemiologic studies in France (Fromont et al. 1997) and Canada (Little et al. 2011) have identified higher infection prevalence in developed areas compared to more rural areas, but prevalence in my study did not differ by habitat of capture location (28% in
natural locations and 29% in urban locations). Therefore, Russellville’s hotspot is indicative of a higher concentration of infected cats in this urbanized local area, but not higher infection prevalence throughout the developed areas relative to natural areas in the city.

Models of FeLV dynamics indicate transmission rates depend on the size of the feral cat population and the relationship between cat density and patterns of contact among cats (Fromont et al. 1998). Availability and distribution of food resources lies on a spectrum with urban areas generally having abundant, clumped food in the form of refuse and artificial feeding stations and the sparsely distributed food in undeveloped landscapes. Areas with dense resources support large, high-density cat populations and high frequencies of contact between individual cats, and therefore have higher prevalence of FeLV than undeveloped areas (Fromont et al. 1998). Within Russellville’s virus hotspot, the majority of trapping locations (92%) were at or near restaurants or known feeding stations, but 71% of trapping locations outside of the hotspot were in natural areas with no known artificial food sources nearby. In addition, catch per unit effort was 3 times greater in urban areas than in natural areas, resulting in the majority of the feral cats that I tested for FeLV and FIV having been captured in urban locations. Further testing of feral cats in natural areas would determine if no difference in infection prevalence of cats in urban and natural areas truly exists in Russellville or if the results from this study stem from the smaller sample sizes in natural areas compared to urban areas.
Survival

Censored individuals occur in many feral cat telemetry studies because cats disperse from study areas, are removed by humans, or suffer undetected mortalities (Kalz et al. 2000, Centonze and Levy 2002, Baker et al. 2010). Less than half (42%) of all censoring of cats occurred over the first 92% of my study period, which was consistent with the number of censored feral cats in other survival studies (Kalz et al. 2000, Centonze and Levy 2002). The remaining 58% of censors happened during the last 5 weeks of 2013. Given that December 2013 was the coldest month during the study, radiocollar failure was the most probable explanation for the loss of radio signal from those censored cats.

I observed few known mortalities of feral cats in Russellville. My calculated naïve survival for feral cats in this study was within the range of survival estimates reported in other feral cat studies, but the modeled survival rate was higher (Kalz et al. 2000, Schmidt et al. 2007, Horn et al. 2011). Given that only female cats experienced known mortalities, sex of the cat had the strongest effect on annual survival. This may reflect the hardships associated with parturition and raising young, but it is more likely the result of demographic stochasticity. Schmidt et al. (2007) reported higher rates of survival for female feral cats (0.88) than male cats (0.52), but they also observed more mortalities ($n = 8$) during their study despite the smaller sample size ($n = 20$) and slightly shorter study period (14 months). Half of the mortalities observed in this study and in Horn et al.’s (2011) study were from unknown causes, but Schmidt et al. (2007) reported vehicle collisions as the major cause of mortalities.
To my knowledge, this is the first published study of FELV and FIV infection prevalence and survival of feral cats in an exurban area. Overall, the biggest limitations regarding these analyses were the small sample sizes and short temporal scale that prevented detailed analyses of trends in FeLV and FIV prevalence and ability to extrapolate results to other exurban areas. Also, larger sample sizes and a longer study period would have identified if the observed mortalities resulted from demographic stochasticity and provided more accurate modeling of the parameters that influence survival of feral cats. Although the small spatial scale and sample size of this study prevents extrapolation to other exurban areas, this case study can be used comparatively with future feral cat research in other exurban areas. Additionally, research at the local level should provide sufficient information and incentives for Russellville’s municipal governments to consider developing a feral cat management plan.

Management Recommendations

High prevalence of FeLV and FIV in the Russellville feral cat population suggests free-roaming pet cats and potentially native wild felids may have high risk of infection in the Russellville area. Currently, feral cats in Russellville are unmanaged, but the combination of high infection prevalence and high survival rates indicates a need for a comprehensive feral cat management plan at the city level. Control of feral cats is among the most contentious and widely debated issues in animal control, yet few governments or private agencies implement comprehensive management efforts (Levy and Crawford 2004).

The efficacy of different management strategies for reducing FeLV and FIV in feral cat populations is understudied, but removal of infected cats and vaccinating
uninfected cats against FeLV and FIV is assumed to be the best practice (Little et al. 2011). Some researchers suggest that FeLV and FIV infection rates in feral cats are similar to infection rates in free-roaming pets so feral cats do not pose increased risk to pets (Nutter 2005, Levy et al. 2008). Instead of removal, Levy et al. (2008) recommend the implementation of trap-neuter-release programs and programs that allow cat owners affordable spay/neuter surgeries, FeLV/FIV tests, and vaccines. I was unable to determine if pet cats in Russellville have a similar infection prevalence to feral cats in the area because the Arkansas Department of Public Health, State of Arkansas Veterinary Medical Examining Board, and the Arkansas Veterinary Medical Association do not maintain records of FeLV/FIV testing or vaccinations in the state (S. Weinstein DVM, Arkansas Department of Health, personal communication). Yet, relative to pet cats, feral cats have larger home ranges, shift their home range seasonally, and show overall higher levels of activity (Horn et al. 2011) and these differences in space use by feral cats probably increases their frequency of encountering new cats. A combination of spay/neuter programs and removal is likely the most practical option to reduce infection prevalence and, depending on the intensity of management, reduce the size of the feral cat population (Nutter 2005). This combination of control techniques is thought to be effective in other wild carnivores (Nutter 2005).

Regardless of the management strategy implemented, education of veterinarians and the public about FeLV and FIV risks and importance of testing and vaccinations for pet cats is paramount. Research indicates that only 54% of veterinarians in the United States followed recommendations regarding educating cat owners and following-up with owners to encourage compliance with the full series of FeLV and FIV tests and vaccines
(Little et al. 2011). In Arkansas, the state does not maintain records of FeLV and FIV testing or vaccinations in pet cats because these viruses are not zoonotic (S. Weinstein DVM, Arkansas Department of Health, personal communication). A survey of veterinarians within Russellville and throughout Arkansas would identify the efficacy of local veterinary protocols regarding education of cat owners and compliance with testing and vaccination recommendations. Pet owners having doorstep food and other people who facilitate artificial feeding stations for feral cats should also be aware of the potential for increased risks of contact and virus transmission around clumped food resources (Chapter 2; Fromont et al. 1998). Educating local pet supply store and pet boutique employees may help spread the information to pet owners who may not employ regular medical care for their cats. Encouraging effective refuse containment by businesses and residences would reduce the abundance of food resources to ultimately reduce the frequency of contact among feral cats and aid management effort.

Nearly 2 dozen trap nights were expended to capture each cat in my study, which is considerably higher than trap effort in other feral cat studies (8.9 – 10.6 trap nights/cat; Short et al. 2002, Levy et al. 2008, Nutter et al. 2004). Throughout the course of this study, I observed a few characteristics of trap locations that appeared to influence trap success. For instance, I had nearly 3 times higher trapping success in urban locations relative to natural locations. Urban living cats are most likely acclimated to anthropogenic objects and are more accustomed to climbing in or through these objects to obtain food compared to cats who occupied natural locations. Thus, feral cat trapping efforts for either removal or trap-neuter-release will likely be more efficient in developed areas than natural locations because of the cats’ willingness to enter a trap to obtain food.
However, several locations where I attempted to trap feral cats that had constant access to feeding stations were unsuccessful, indicating that too much access to food will likely result in cats being satiated and therefore unwilling to enter traps regardless of their acclimation to anthropogenic objects. In these locations, managers can attempt to gain cooperation from the people who provide the food (i.e., requesting that feeding station caretakers suspend feeding for a few days), which will likely increase trapping success. The greater trapping success in urban areas suggests that providing supplemental food to cats in natural areas may increase trappability. However, providing supplemental food may also increase contact among individuals, possibly increasing rates of virus transmission, and may facilitate higher feral cat fecundity and survival by providing a stable food source. When trapping feral cats in natural areas, the best course of action is probably to set up anthropogenic objects (i.e., boxes, traps, food dishes) and provide supplemental food in and around these objects for periods of time long enough for cats to become acclimated, but not so long that it initiates a population increase.

Feral cat management requires a community effort because there are many stakeholder groups. Effective feral cat management, whether lethal or non-lethal, requires long-term, intensive efforts because cats are prolific breeders and elusive (Nutter 2005). Just a few intact individuals remaining in a colony after management can repopulate the group rapidly and abandoning pet cats is a common practice, so intact cats may be added to a population continuously (Nutter 2005). Considering the effort required to control feral cats throughout the entire city, concentrating management and education efforts in the portion of Russellville encompassed by the virus hotspot may be the most economical solution.
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Table 1.1. Infection prevalence (%) of feline leukemia virus (FeLV) and feline immunodeficiency virus (FIV) and regional variation within feral and stray cat (*Felis catus*) populations.

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<td>Urban Italy</td>
<td></td>
<td>Feral</td>
<td>---a</td>
<td>28.60</td>
</tr>
<tr>
<td>Natoli et al. 2005</td>
<td>Urban France</td>
<td>Feral</td>
<td>---a</td>
<td>19.00</td>
</tr>
</tbody>
</table>

*Data not included in this study.
Table 1.2. Variable abbreviations, descriptions, and binomial numbers assigned to each covariate for a priori models to evaluate survival of exurban feral cats (*Felis catus*) in Russellville, Arkansas, 2012 – 2014.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Abbreviation</th>
<th>Description (assigned binomial covariate)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body condition score</td>
<td>BCS</td>
<td>Continuous variable ranging 1-9</td>
</tr>
<tr>
<td>Habitat of capture location</td>
<td>Hab</td>
<td>Natural (0) or urban (1)</td>
</tr>
<tr>
<td>Virus infection status</td>
<td>Vir</td>
<td>Uninfected (0); or positive for FeLV, FIV, or FeLV/FIV (1)</td>
</tr>
<tr>
<td>Season in which mortality occurred</td>
<td>Seas</td>
<td>Warm: Apr – Oct (0) or cold: Nov – Mar (1)</td>
</tr>
<tr>
<td>Sex of the cat</td>
<td>Sex</td>
<td>Male (0) or female (1)</td>
</tr>
</tbody>
</table>
Table 1.3. A priori models for estimating survival of exurban feral cats (*Felis catus*) in Russellville, Arkansas, 2012 – 2014. Table includes unstandardized parameter estimates and standard error, the number of parameters (*K*), Akaike Information Criterion values adjusted for small samples (*AICc*), distance from the lowest *AICc* values (Δ*AICc*), Akaike model weights (*ω*), and model deviance (Dev) used to evaluate models. Descriptions of variables are in Table 1.2.

<table>
<thead>
<tr>
<th>Model</th>
<th><em>K</em></th>
<th><em>AICc</em></th>
<th>Δ<em>AICc</em></th>
<th><em>ω</em></th>
<th>Dev</th>
</tr>
</thead>
<tbody>
<tr>
<td>22.95±0.00(Intercept) – 17.85±0.00(Sex)</td>
<td>2</td>
<td>52.87</td>
<td>0.00</td>
<td>0.31</td>
<td>48.86</td>
</tr>
<tr>
<td>21.19±0.00(Intercept) – 16.70±0.00(Sex) + 0.99±1.00(Hab)</td>
<td>3</td>
<td>53.95</td>
<td>1.08</td>
<td>0.18</td>
<td>47.93</td>
</tr>
<tr>
<td>21.59±0.00(Intercept) – 16.62±0.00(Sex) + 0.25±1.00(Seas)</td>
<td>3</td>
<td>54.82</td>
<td>1.95</td>
<td>0.12</td>
<td>48.80</td>
</tr>
<tr>
<td>5.71±0.50(Intercept)</td>
<td>1</td>
<td>55.73</td>
<td>2.86</td>
<td>0.07</td>
<td>53.72</td>
</tr>
<tr>
<td>22.40±0.00(Intercept) – 18.03±0.00(Sex) + 0.24±1.00(Seas) + 0.98±1.00(Hab)</td>
<td>4</td>
<td>55.91</td>
<td>3.04</td>
<td>0.07</td>
<td>47.87</td>
</tr>
<tr>
<td>4.81±0.71(Intercept) + 1.37±1.00(Hab)</td>
<td>2</td>
<td>55.99</td>
<td>3.12</td>
<td>0.06</td>
<td>51.98</td>
</tr>
<tr>
<td>1.55±4.29(Intercept) + 0.85±0.90(BCS)</td>
<td>2</td>
<td>56.81</td>
<td>3.94</td>
<td>0.04</td>
<td>52.80</td>
</tr>
<tr>
<td>28.78±0.00(Intercept) – 16.94±0.00(Sex) + 2.68±1.83(Hab) + 0.34±1.03(Seas) – 1.68±1.27(BCS) – 1.49±1.09(Vir)</td>
<td>6</td>
<td>56.99</td>
<td>4.12</td>
<td>0.04</td>
<td>44.92</td>
</tr>
<tr>
<td>6.06±0.71(Intercept) – 0.87±1.00(Vir)</td>
<td>2</td>
<td>57.00</td>
<td>4.13</td>
<td>0.04</td>
<td>52.99</td>
</tr>
<tr>
<td>5.63±0.71(Intercept) + 0.17±1.00(Seas)</td>
<td>2</td>
<td>57.71</td>
<td>4.84</td>
<td>0.03</td>
<td>53.70</td>
</tr>
<tr>
<td>4.74±0.86(Intercept) + 1.37±1.00(Hab) + 0.13±1.00(Seas)</td>
<td>3</td>
<td>57.98</td>
<td>5.11</td>
<td>0.02</td>
<td>51.96</td>
</tr>
<tr>
<td>1.88±4.49(Intercept) + 0.85±0.93(BCS) – 0.83±1.00(Vir)</td>
<td>3</td>
<td>58.15</td>
<td>5.28</td>
<td>0.02</td>
<td>52.13</td>
</tr>
</tbody>
</table>
Figure 1.1. Trapping locations for exurban feral cats (Felis catus) in Russellville, Arkansas 2012 – 2014. All locations include a 250m buffer so that small locations would be visible at this scale. Locations outside of city limits are parks managed by the City of Russellville.
Figure 1.2. Infection prevalence (%) of feline leukemia virus (FeLV) and feline immunodeficiency virus (FIV) by sex of the cat, habitat at capture location, and body condition scores (BCS; ≤4 is underweight, 5 is ideal, and ≥6 is overweight) of feral cats (*Felis catus*) in Russellville, Arkansas 2012 – 2014. There were no differences of infection prevalence within groups ($G_{1,2} = 0.02 – 1.48$ $P = 0.224 – 0.894$).
Figure 1.3. Infection hotspot in Russellville, Arkansas 2012-2014 as determined by 50% kernel density area of all feral cats (*Felis catus*) that tested positive for feline immunodeficiency virus, feline leukemia virus or both viruses.
CHAPTER 2:

POPULATION DENSITY AND CHARACTERISTICS OF ANNUAL AND SEASONAL SPACE USE BY FERAL CATS IN AN EXURBAN AREA

Feral cats have the ability to exploit a wide range of environments (Longcore et al. 2009, Loyd and Miller 2010) from wilderness habitats (Jones and Coman 1982, Norbury et al. 1998, Harper 2007) to highly urbanized areas (Calhoon and Haspel 1989, Devillard et al. 2003, Schmidt et al. 2007, Tennent and Downs 2008). This broad ability to adapt results in large variations in spatial and social structure (Genovesi et al. 1995, Say et al. 1999, Devillard et al. 2003, Schmidt et al. 2007) which is influenced primarily by the abundance and dispersion of food resources (Genovesi et al. 1995, Liberg et al. 2000, Crowell-Davis et al. 2004, Tennent and Downs 2010). Suburban and urban habitats have patchy areas of abundant food resources in the form of garbage sites and feeding stations provided by humans (Say et al. 1999, Liberg et al. 2000, Bonanni et al. 2007, Tennent and Downs 2008) that support high-density cat populations (≥50 cats/km²; Genovesi et al. 1995, Liberg et al. 2000). However, food resources in rural and wilderness habitats are more dispersed and likely of natural origin (Genovesi et al. 1995) which support only low-density populations of cats (≤5 cats/km²; Genovesi et al. 1995, Liberg et al. 2000).

Home range areas of feral cats vary greatly for both sexes (0.27 – 620ha; Liberg et al. 2000) and male cats tend to occupy larger areas than females (Table 2.1; Jones and Coman 1982, Harper 2007, Schmidt et al. 2007, Guttilla and Stapp 2010, Horn et al. 2011). However, the general trend is that home ranges of feral cats decrease in size as cat density increases (Table 2.1; Liberg et al. 2000, Harper 2007, Tennent and Downs 2008).
Cats living at high densities form bachelor, bachelorette, or mixed social groups (i.e., colonies) and have overlapping home ranges concentrated around food sources (Genovesi et al. 1995, Fromont et al. 1998, Say et al. 1999, Edwards et al. 2001, Devillard et al. 2003, Bonanni et al. 2007, Tennent and Downs 2008). Cats at low densities are generally solitary and their home ranges do not overlap (Fromont et al. 1998, Say et al. 1999, Edwards et al. 2001, Devillard et al. 2003, Tennent and Downs 2008). However, exceptions to these trends were reported in Brooklyn, NY where feral cats in 2 high-density populations (mean 488 and 203 cats/km²) remained solitary except females with young (Calhoon and Haspel 1989). Alternatively, 2 unsubsidized female cats in a low-density (3.5 cats/km²) cat population in New Zealand lived together in a barn except during the breeding season (Liberg et al. 2000).

The understanding of how organisms use habitats is central to the study of animal ecology (Johnson 1980), but research into feral cat habitat use in the United States has been limited to urban areas (Schmidt et al. 2007, Horn et al. 2011). In a Texas urban area, feral cats utilized patchy forested areas located at the edge of the urban study area where human population density was low (Schmidt et al. 2007). In Illinois, a study conducted in an urban community surrounded by agricultural lands determined that annual home ranges for feral cats included grasslands more than was expected based on habitat availability (Horn et al. 2011). Yet, in this study, seasonal home range use varied with cats using urban industrial areas during summer more than expected based on habitat availability but in fall and winter they used farms more than expected (Horn et al. 2011). The habitats that cats used less than expected based on availability were forests during summer and fall, urban residential areas in fall and winter, and row crops.
throughout the year (Horn et al. 2011). Unlike urban development, exurban areas are typically adjacent to natural areas (Hansen et al. 2005) providing feral cats with more choices of habitat, and therefore, animals residing in exurbia may use habitats differently than urban animals.

Although feral cat populations have been studied extensively in urban (Calhoon and Haspel 1989, Mitchell and Beck 1992, Nutter et al. 2004, Schmidt et al. 2007, Schmidt et al. 2009; Champaign and Urbana, IL: Horn et al. 2011) and rural (Mitchell and Beck 1992, Nutter et al. 2004) areas, information regarding exurban feral cats is sparse. Given that suburban and urban areas tend to support high-density cat populations while rural areas support low-density cat populations (Genovesi et al. 1995, Liberg et al. 2000), then exurban areas theoretically should have cat populations intermediate in size (5 – 50 cats/km²; Genovesi et al. 1995, Liberg et al. 2000). It also follows that exurban cats should have home range areas intermediate (0.84 – 2.62ha) to the large home ranges reported for cats at low densities and small home ranges for cats at high densities (Genovesi et al. 1995, Liberg et al. 2000). Understanding feral cat habitat use at various spatial and temporal scales is an important step towards filling the knowledge gaps about feral cat ecology within a given environment. My objectives in this chapter were to quantify annual and seasonal home range areas and estimate density of feral cats in an exurban area. I also characterized macrohabitat use of seasonal and annual home ranges. Such knowledge could be invaluable for feral cat management efforts to protect native wildlife and reduce health risks to humans and their pets in exurban areas.
METHODS

Study Area

Please see the study area description in Chapter 1.

Capture and Animal Handling

Please see the capture and animal handling methods described in Chapter 1.

Radiotelemetry

I used an R410 receiver (ATS), a hand-held 3-element Yagi antenna (ATS), and ground-based radiotelemetry techniques to track all radiocollared cats and to determine home range area and core area use. I commenced tracking radiocollared feral cats 2 weeks post collar deployment and continued through 30 December 2013. I triangulated the location of each cat 2 – 3 times per week by obtaining 3 – 5 azimuths (Horn et al. 2011) collected <20 min to minimize error resulting from cat movement (Guttilla and Stapp 2010, Byrne and Chamberlain 2011). I systematically collected points for each cat by rotating through 6 4-hour time blocks (0001 – 0400hr, 0401 – 0800hr, 0801 – 1200hr, 1201 – 1600hr, 1601 – 2000hr, and 2001 – 0000hr) obtaining approximately equal number of points per cat in each time block to provide an unbiased representation of the cat’s movement patterns (Aebischer et al. 1993). If I visually detected a radiocollared cat during tracking, I used GPS to record its location. While conducting telemetry, I recorded the GPS locations of known feeding stations and refuse containers within the home ranges of collared feral cats because there may be a positive relationship between concentrated urban food sources and overlapping feral cat home ranges (Liberg et al. 2000, Harper 2007, Tennent and Downs 2008).
Home Range Area

I calculated 9 estimates of home range for each radiocollared cat for which I had collected ≥30 locations for both warm (Apr – Oct) and cold (Nov – Mar) seasons (Seaman et al. 1999). First, I used Location of a Signal (LOAS; Ecological Software Solutions LLC, Florida) to convert telemetry points and azimuths data to cat locations. Second, I used ArcGIS to create 3 separate shapefiles for each cat: 1 containing all locations from the study for annual home range; 1 for all locations collected during the warm season; and 1 for all locations collected during the cold season. I then calculated annual and seasonal (i.e., both warm and cold season) home range estimates for each cat from these 3 sets of shapefiles.

For each annual and seasonal home range estimate, I calculated 2 measures of home range (95% minimum convex polygon [MCP] and 95% kernel density estimator [KDE]) and 1 measure of core home range (core). Minimum convex polygon is a commonly used estimator of feral cat home ranges (Edwards et al. 2001, Harper 2007, Schmidt et al. 2007, Guttilla and Stapp 2010, Horn et al. 2011), but a major disadvantage is that all outermost locations are included in the convex polygon. Thus, locations that may be considered extraterritorial excursions are included and could inflate home range size (Edwards et al. 2001, Franzreb 2006). I considered the outermost 5% of locations for each cat to be outliers and used the Mean Center and Near tools in ArcGIS to identify and remove these points. Then I used GME with ArcGIS to calculate MCP (GENMCP command). Conversely, KDE uses locations to estimate the probability that a cat will be located within isopleths of varying percentages and can provide information about how intensively a cat uses portions of its home range (Hemson et al. 2005). Therefore, I also
used GME to calculate 95% KDE (KDE and ISOPLETH [quantile = 0.95] commands) to estimate home range area and 50% KDE (ISOPLETH command [quantile = 0.50]) to identify core areas (i.e., where the cat spends a disproportionate amount of time within their home range; Guttilla and Stapp 2010, Schmidt et al. 2007).

After calculating the 9 home range estimates for each cat, I ran a 1-way ANOVA with Tukey’s HSD test for pairwise comparisons (PROC GLM; SAS Institute, Cary, North Carolina; Sokal and Rohlf 1995) to compare the annual, warm season, and cold season estimates within the type of estimator (e.g., annual 95% KDE vs. warm 95% KDE vs. cold 95% KDE) and between estimators for each season (e.g., annual 95% KDE vs. annual 95% MCP vs. annual core). I also determined if home range size differed between sexes, virus infection status (Chapter 1), and BCS (Chapter 1) (Guttilla and Stapp 2010, Byrne and Chamberlain 2011, Horn et al. 2011).

**Macrohabitat Use**

Tennent and Downs (2008) determined that home ranges of feral cats in areas subsidized with food were smaller than home ranges of cats not receiving supplemental food. To determine if food subsidies influenced feral cat home range size in Russellville, I created a layer of point locations of all artificial food sources I observed while conducting radiotelemetry on the cats. Next, I overlaid the MCP, KDE, and core home range polygons for each cat onto this data layer. I log transformed home range and core areas to meet the assumption of normality, and then used 9 separate linear regressions (PROC REG; \( \alpha = 0.05 \)) to determine if the size of the logged area of each of the home range estimates (e.g., warm 95% KDE, annual MCP, cold core) was affected by the number of food sources within home ranges. I also wanted to determine if the number of
food sources influenced the amount of home range overlap by feral cats that occupied the same space. Therefore, I used the Clip tool in ArcToolbox to calculate the area of overlapping KDE home ranges between neighboring feral cats and quantified the number of known artificial food sources within each overlapping area. Then, I regressed the log area of range overlap on the number of known artificial food sources within the shared spaces. For all linear regressions, I used residual plots and the Shapiro-Wilk statistic to evaluate assumptions.

I used compositional analysis to investigate annual and seasonal macrohabitat use by feral cats in Russellville (Aebischer et al. 1993, Harper 2007, Byrne and Chamberlain 2011, Castillo et al. 2011). I used ArcGIS and the National Land Cover Database 2011 (NLCD; Jin et al. 2013) to create a data layer of Russellville’s 5 major land cover types (Figure 2.1). I then overlaid roads and railroads onto this layer using 2012 TIGER/Line Shapefiles (United States Census Bureau 2012). I compared the habitat composition by quantifying the number of point locations within each habitat for annual and seasonal KDE home ranges and habitats available within the study area (2nd order use; Johnson 1980). Research into 2nd order use of any species typically defines the available habitat as an arbitrary measure of the study area (Beasley et al. 2007). However, if animals are monitored in only a small portion of the defined area and the habitat composition between the overall study area is different from the region where monitored animals occurred, that measure of habitat availability may be biased (Beasley et al. 2007). Therefore, I used all telemetry points from all feral cats that were included in 2nd order analyses to construct a 100% MCP and used a G-test (PROC FREQ) to compare land cover within the 100% MCP and Russellville. Land cover composition within the 100%
MCP differed from the composition of Russellville \( (G_5 = 442.23 \ P < 0.001) \), so I used the 100% MCP as the defined study area for 2\textsuperscript{nd} order analysis in lieu of the entire city (Beasley et al. 2007). I also quantified point locations within habitats of the core areas to compare with the number of point locations within habitats of the annual and seasonal KDE home ranges (3\textsuperscript{rd} order use; Johnson 1980; Chamberlain et al. 2003).

Compositional analysis requires calculation of log-ratios of habitat use versus availability and 0 is not valid in log-ratio transformations (Aebischer et al. 1993). Moreover, substituting 0 with small values (i.e., 0.0001) can potentially inflate Type I error rates and misclassification rates (Bingham and Brennan 2003). Therefore, I substituted observations of 0 use in a given habitat at the 2\textsuperscript{nd} order scale with 0.3 as suggested by Bingham and Brennan (2003). Habitats used at the 2\textsuperscript{nd} order scale also represented available habitats at the 3\textsuperscript{rd} order scale. Therefore, for 3\textsuperscript{rd} order analyses, I used 0.3 as the availability for any habitat not represented within the home range and for habitats not used within the core area, I substituted 0 with a number 1 order of magnitude smaller than the smallest nonzero value from the corresponding available habitat (Aebischer et al. 1993). The habitat type classified as “other” was used at the 2\textsuperscript{nd} order scale by only 1 cat and comprised <1% of the cat’s total KDE. In addition, “other” was not used by any cats at the 3\textsuperscript{rd} order scale. Given that “other” comprised 0.8% of the 2\textsuperscript{nd} order study area and that the majority of cats were not observed using this habitat, I excluded it from analyses (Aebischer et al. 1993).

I conducted 3 multivariate analyses of variance (MANOVA; PROC GLM) for both 2\textsuperscript{nd} and 3\textsuperscript{rd} orders of habitat use to detect annual and seasonal differences between log-ratio habitat use and availability percentages (dependent variables) by sex of the cat,
virus infection status of the cat, and land cover type (independent variables; Byrne and Chamberlain 2011). If a significant difference existed between habitat availability and use for an independent variable, then I performed a ranking matrix of $t$-tests to identify how habitat use changed by annual and seasonal use (Aebischer et al. 1993, Castillo et al. 2011).

**Population Abundance**

I used the Schnabel abundance method (Overton 1965) to estimate feral cat population density within the effective trap area. Given that patchy vegetation at trap sites precluded trapping on grids (Chapter 1) and because the home ranges of some cats likely extended beyond the borders of the area encompassed by the outermost traps (Dillon and Kelly 2008, Balme et al. 2009), I determined the effective trap area by creating a shapefile in ArcGIS of all trap locations and establishing a circular buffer equivalent to the mean annual KDE home range area around each trap (Lancia et al. 2005, Dillon and Kelly 2008, Balme et al. 2009). This method of calculating effective trap area has proven more accurate for estimating densities of ocelots (*Leopardus pardalis*; Dillon and Kelly 2008) and other cryptic carnivores (Balme et al. 2009) compared to methods of establishing effective trap areas based on the outer most traps or by establishing buffers equal to half the mean maximum distance moved by animals. I used the Merge tool in ArcGIS to combine all overlapping buffers into a single shapefile, quantified the land area encompassed by the trap area, and extrapolated feral cat population abundance within Russellville. I also calculated Schnabel population abundance for feral cats captured in natural and urban locations, used the mean annual KDE home range area to estimate effective trap area in these different location types, and
then extrapolated feral cat population densities to compare with urban and rural densities reported in other feral cat studies.

RESULTS

I tracked 29 feral cats for 65 weeks (mean ± SE throughout: 41.86 ± 0.58 weeks/cat) and obtained 2,365 point locations (81.55 ± 5.93 locations/cat). However, I excluded 11 cats from home range and macrohabitat analyses because I recorded <30 point locations during the warm or cold season for each cat (Seaman et al. 1999, Chamberlain et al. 2002, Bingham and Brennan 2003). Of the remaining 18 cats (10 females, 8 males), 5 were positive for FeLV and/or FIV, 13 tested negative for these viruses, 16 were captured in urban areas of the city, and only 2 were captured in natural areas.

Home Range Area

The mean number of locations for KDE and core areas were slightly greater than the number of MCP locations because calculation of 95% MCP required removing the outermost 5% of locations (Table 2.2). The KDE and MCP home ranges were larger than core areas for annual and seasonal estimates ($F_{8,149} = 22.31 \ P < 0.001$). The KDE estimates were larger than the MCP estimates for the cold season, but these estimators did not differ for the annual or warm season estimates. Annual and seasonal home ranges were insignificant from one another within the KDE, MCP, and core estimates. However, 1 cat’s core range during the warm season was 3 times the size of the next largest warm season core range and when it was experimentally removed, core areas in the cold season were larger than in the warm season ($F_{2,50} = 7.11 \ P = 0.002$). Annual core areas were not different from either cold or warm seasons.
Home range estimates were influenced by the sex of the cats (Table 2.3), but not by infection status (i.e., positive for FeLV and/or FIV; negative for FeLV and FIV; Table 2.4) or BCS. Male cats had larger home ranges than female cats ($F_{1,149} = 41.88 \ P < 0.001$). Home range estimates for feral cats that tested positive for FeLV and/or FIV were not different from home range areas of uninfected cats ($F_{1,149} = 0.19 \ P = 0.664$). Cats also did not differ in home range estimates based on BCS ($F_{2,149} = 2.31 \ P = 0.103$).

**Macrohabitat Use**

I identified 43 artificial food sources (25 dumpsters, 18 feeding stations) mostly located in medium-high intensity development (67.44%) and open-low intensity development (27.91%) land covers within Russellville. The number of known artificial food sources located within annual and cold home ranges did not have an effect on the KDE and MCP home range estimates ($F_{1,16} = 0.08 - 1.27 \ P = 0.276 - 0.783$). During the warm season, the number of known food sources within home ranges had a positive effect on the size of the KDE ($\beta = 0.27 \pm 0.10$) and MCP estimates ($\beta = 0.32 \pm 0.15; F_{1,16} = 4.81 - 7.08 \ P = 0.017 - 0.043$). The number of food sources within core areas did not have an effect on home range size during the warm and cold seasons ($F_{1,16} = 0.01 - 2.68 \ P = 0.121 - 0.930$). There was some evidence indicating that as the number of known food sources increased ($\beta = 0.37 \pm 0.18$), the size of the annual core home range also increased ($F_{1,16} = 4.43 \ P = 0.052$).

Of the 18 feral cats used in home range analyses, 13 shared some portion of their annual KDE home ranges with $\leq 2$ other radiocollared cats. The average amount of shared area was $6.84 \pm 1.44$ha and included $1.77 \pm 0.43$ food subsidies. The size of the overlapping KDE areas increased ($\beta = 0.33 \pm 0.15$) as the number of shared food
subsidies increased \((F_{1,11} = 4.99 \ P = 0.047)\).

At the 2\textsuperscript{nd} order home range scale, habitat use by sex of the cat (Wilks’ \(\lambda = 0.48 F_{3,50} = 0.48 \ P = 0.695\)) did not differ from random, but habitat use by land cover type (Wilks’ \(\lambda = 0.66 F_{6,98} = 3.71 \ P = 0.003\)) and by infection status of the cat (Wilks’ \(\lambda = 0.67 F_{3,50} = 8.09 \ P < 0.001\)) were nonrandom. I identified 1 – 2 outliers in each of these MANOVA tests, but post hoc removal of the outliers did not alter the outcomes. In general, open-low and medium-high intensity developed habitats were interchangeable for land cover type both annually and seasonally. For land cover type during the annual and warm season, the rank of habitats used by feral cats ordered: open-low intensity development > medium-high intensity development > pasture and hay fields > forest (Table 2.5). There was no detectable difference in use of open-low, medium-high, or pasture and hay field habitats, nor was pasture and hay field use different from forest habitat; however, open-low and medium-high intensity developed areas were used significantly more than forests. The only difference between the annual and warm season rank order and cold season rank order was that medium-high intensity development and open-low intensity development ranks were reversed. There was no detectable difference in any of the land cover types except forest areas and pasture and hay fields were used significantly less than medium-high intensity developments.

Both infected and uninfected feral cats used open-low and medium-high intensity development interchangeably (Table 2.6), however, their rank order and use of other land covers were slightly different. The rank order of habitat use by feral cats that tested positive for FIV and/or FeLV did not change between annual, warm, and cold seasons: medium-high intensity development > open-low intensity development > pasture and hay fields. 
fields > forest. Infected cats consistently used both developed areas and pasture and hay fields interchangeably with only the intensity of forest habitat use changing slightly between annual and seasonal time frames. Annual habitat use by cats not infected with FIV or FeLV ordered: open-low intensity development > medium-high intensity development > forest > pasture and hay field. Unlike infected cats, uninfected cats used both developed areas significantly more than pasture and hay fields within the annual home range. Annual forest use among uninfected cats was equal to pasture and hay field and medium-high intensity developed areas, but less than open-low intensity developments whereas infected cats used forest habitat less than both developed areas. During the warm season, the rank of habitats used by uninfected cats ordered: open-low intensity development > medium-high intensity development > pasture and hay field > forest. Uninfected cats still used the developed areas interchangeably and use of pasture and hay field and forest habitats were equal to medium-high intensity developed areas, but less than open-low intensity developments. Comparatively, warm season forest use among infected cats was less than use of the developed areas and pasture and hay fields. During the cold season, uninfected cats used habitats in the order: medium-high intensity development > open-low intensity development > forest > pasture and hay field. Once again, these cats used the developed areas interchangeably during the cold season, but forest habitat use was also equal to developed areas while pasture and hay fields were used less than the developed habitats. Forest use by infected cats during the colds season was the same as annual use.

At the 3rd order home range scale, habitat use by sex of the cat (Wilks’ $\lambda = 0.95$ $F_{3,50} = 0.94$ $P = 0.427$) and virus infection status of the cat (Wilks’ $\lambda = 0.95$ $F_{3,50} = 0.96$ $P$
were random, but use by land cover was nonrandom (Wilks’ $\lambda = 0.33$ $F_{6,98} = 11.98$ $P < 0.001$). I identified 1 outlier in each MANOVA test, but post hoc removal of the outliers did not alter the outcomes. Within their core areas, cats did not use the land cover types differently among the seasons (Table 2.7). The relative order and significance of use was the same as the annual and warm season 2$^{nd}$ order analyses.

**Population Abundance**

Given the mean annual KDE estimate of $0.1976\text{km}^2$ for all cats, I used ArcGIS to create a 444.52m buffer around each trap to obtain an effective trap area of 2,495.94ha. I used the Schnabel method to estimate population abundance within the effective trap area at 245 feral cats (0.10 cats/ha) which was then extrapolated to 719 cats estimated to reside within Russellville. Effective trap area and Schnabel abundance in the natural locations were 1,101.73ha and 84 cats (0.08 cats/ha), respectively. Conversely, the effective trap area in urban locations summed to 1,394.22ha and abundance was 144 (0.10 cats/ha).

**DISCUSSION**

Given that feral cat ecology is understudied in exurban areas, my research objectives were to estimate feral cat density, quantify annual and seasonal home range areas, and characterize macrohabitat use among annual and seasonal home ranges of feral cats in the exurban city of Russellville, Arkansas. Home ranges of male feral cats were larger than female home ranges. The number of known feeding stations appeared to influence warm season home range size and the amount of overlap between annual home ranges of neighboring cats. Analyses of habitat use by feral cats at the 2$^{nd}$ and 3$^{rd}$ order scales for annual and seasonal home ranges indicated that cats use developed habitats
more than expected based on availability and forests much less than expected based on availability. At the 2nd order scale, cats infected with FIV and/or FeLV tended to use pasture and hay fields more than forested compared to uninfected cats. These results are the beginning of filling the gaps in literature about exurban feral cat ecology and may serve as a basis for comparison in future studies of exurban cats.

**Home Range Area**

Both MCP and KDE are commonly reported for feral cat home ranges although the 2 calculations typically yield similar results (Schmidt et al. 2007, Guttilla and Stapp 2010, Horn et al. 2011). In this study, annual and warm season MCP and KDE home ranges were not different, but cold season KDE ranges were larger than MCPs. This difference in KDE and MCP suggest that feral cats used the periphery of their home ranges more intensely than the center area during the cold season. Differences among annual and seasonal home range sizes within the estimator type (i.e., annual KDE vs. warm KDE vs. cold KDE) of feral cats in Russellville were not apparent, however a post-hoc analysis revealed that core areas were larger in the cold season than in the warm season. Seasonal shifts in home range sizes reported in the literature appear to vary by location and definition of seasons. For instance, Horn et al. (2011) observed no difference in range sizes across summer, fall, or winter seasons in rural Illinois, but Guttilla and Stapp (2010) observed larger range sizes for male cats than females during the wet season on a California island. Cats in Russellville may utilize a larger core area during cooler temperatures potentially because they do not run the same risk of overheating in the cold season compared to the warm season.
Home range sizes for feral cats vary greatly, but generally they have an inverse relationship with feral cat density and male cats typically have larger home ranges than female cats (Liberg et al. 2000, Tennent and Downs 2008). In this study, home range sizes of male cats were within or close to range sizes reported for males living in populations with low density of <30 cats/ha (15 – 620 ha; Liberg et al. 2000). Female cat home ranges were smaller than those reported for females living in low-density populations (19 – 170 ha), but larger than home ranges for medium-density populations (0.84 – 1.77 ha, 300 – 500 cats/ha; Liberg et al. 2000). Core areas were within range of those reported for suburban and urban feral cats in the literature (0.07 – 11.35 ha; Schmidt et al. 2007, Tennent and Downs 2008), but much smaller than core ranges for cats living in the wilderness of Australia (54.00 – 578.60 ha; Norbury et al. 1998, Edwards et al. 2001). These results suggest that feral cat density in Russellville is relatively low and although feral cat overall home ranges are more similar to rural cat populations with dispersed food resources, areas of core use are similar to urban and suburban living cats. Therefore, it appears that this exurban feral cat population shares characteristics with both rural and urban feral cat populations.

Research into differences in space use by cats infected with FeLV or FIV is sparse. In this study, home range sizes of infected cats did not differ from range sizes of cats that tested negative for both viruses. Cats infected with FeLV or FIV may be asymptomatic and therefore not physically weaker than uninfected cats for 80 – 300 days after initial infection (Hofmann-Lehmann et al. 1997, Mari et al. 2004) which may explain the lack of differences in home range sizes. However, it also implies that infected and uninfected cats traverse similar distances and have similar rates of encounter
with other cats, which likely contributes to Russellville’s high virus infection prevalence (Chapter 1).

**Macrohabitat Use**

The number of known artificial food resources did not appear to influence annual or cold season ranges, but had a positive effect on feral cat home ranges during the warm season. In addition, home range overlap between neighboring cats was positively influenced by the number of food sources within the shared space, supporting the assertions that clumped resources support a larger number of cats than distributed resources (Fromont et al. 1998, Bonanni et al. 2007, Tennent and Downs 2008). However, it is likely that I did not encounter and record all artificial food resources within every cat’s home range and therefore food may not be the influence driving warm season home range sizes or home range overlap by feral cats.

The only other study of 2nd order habitat use by feral cats occurred in an area dominated with agriculture that was <40% developed land cover and similar to my results, those authors reported that feral cats used urban and grassland habitats disproportionately to availability (Horn et al. 2011). In general, feral cats in my study used the developed areas at the 2nd order scale disproportionately to availability for annual, warm, and cold seasons, likely because of the concentrated food resources in the forms of poorly-contained refuse and feeding stations provided by humans. Consistency in habitat use among the developed habitat types may also reflect the sample of cats used in this analysis; by excluding cats for which I had collected <30 point locations, 89% of the cats included in the compositional analyses were captured in urban locations. Therefore, the sample size for habitat use was not representative of the entire feral cat
population in Russellville. Forest use was significantly less than use of developed areas in general, whereas pasture and hay use was often interchangeable with the developed land covers. Pasture and hay field use may be slightly higher than forest areas perhaps because of the ground-level cover these areas provide and potentially because thick herbaceous growth provides habitat for ground-dwelling small mammals and ground-nesting birds that cats can depredate more easily than when prey species can escape into trees. In addition, within the 100% MCP used as the study area, forest patches (mean ha ± SE; 1.30 ± 0.24) were smaller than pasture and hay field patches (4.25 ± 1.21) and therefore these pasture and hay field patches likely support larger populations and possibly a greater diversity of prey species than the forest patches (Connor and McCoy 2001).

Horn et al. (2011) also reported that feral cats shifted their habitat use across seasons presumably to reflect availability of protective cover. For example, cats shifted home range areas away from row-crops after fall harvests occurred. Cats in my study slightly shifted away from their use of pasture and hay fields during the cold season, appearing to use medium-high intensity developed land cover more intensely than the relatively natural areas. Relative to pasture and hay field and forest habitats, developed areas provide reliable food resources via feeding stations provided by humans and poorly contained refuse that may help cats meet the energetic requirements for thermoregulation in cold weather. In addition, underneath raised buildings in developed areas, particularly heated buildings, likely provide resting sites that are warmer than resting sites in the more natural locations, further aiding cats’ thermoregulation requirements during the cold season. I examined DRSs during the summer (Chapter 3) and identified underneath
anthropogenic structures as the 2nd most frequently used DRS type, but further research is required to identify how cats use these structures and other potential resting sites during the cold season. Although speculative, cats in this study appeared to shift habitat use according to thermoregulation needs as opposed to protective cover as suggested by Horn et al. (2011).

Use of open-low and medium-high intensity developments were the top ranked habitats and were also interchangeable for both virus infected and uninfected feral cats throughout the year, but the rank order of these habitats shifted. Cats that tested positive for FIV and/or FeLV used medium-high intensity developments slightly more than uninfected cats during annual and warm season; use of this land cover type was ranked 1st for both types of cats during the cold season. This use of highly-developed areas by infected cats is consistent with findings reported in other feral cat studies (Fromont et al. 1998, Little et al. 2011) and from models of infectious diseases (Fromont et al. 1997) where abundant, clustered food sources increase frequency of contact, and therefore virus transmission, among cats. The availability of food resources in medium-high intensity developed habitats reduce the foraging time and effort associated with meeting energetic costs. Infected cats appear to take advantage of these areas year-round whereas uninfected cats utilize these areas mostly during the cold season when prey densities are low in more natural habitats. Moreover, developed areas likely provide warm resting sites, such as underneath heated buildings or within the undercarriage of parked cars, that would aid thermoregulation requirements during the cold season.

In general, feral cats of different virus infection status appeared to frequent the same number of habitats annually and seasonally, but they used forest and pasture and
hay field habitats differently. Infected cats used pasture and hay field habitats interchangeably with the developed areas whereas uninfected cats tended to use pasture and hay fields less than developed areas. However, the pastures and hay fields that I observed infected cats using were adjacent to developed areas containing known feeding stations. Uninfected cats also utilized forest habitats slightly more frequently than infected cats, as compared to the developed land cover types. The observed patterns of habitat use by cats of different virus infection status may result from infected cats being slightly more dependent on artificial food resources than uninfected cats; perhaps, because uninfected cats are in better physical condition and therefore better able to hunt prey. Yet, BCSs did not differ between infected and uninfected cats (Chapter 1) and therefore other variables that I did not examine may be the driving influence habitat use by infected and uninfected cats.

The rank of habitat use by feral cats at the 3rd order scale did not change among annual, warm, and cold seasons. Similar to 2nd order use, the developed areas were interchangeable in their importance and were likely used the most frequently because of the abundant food sources available in these areas and because most of the cats in this analysis were captured in an urban area. Pasture and hay field habitats were also interchangeable with the developed areas, probably for similar reasons of food availability, but in the form of prey animals, as well as the amount of cover provided by vegetation.

**Population Abundance**

Overall cat population density in Russellville was relatively low and this estimate is consistent with population densities of feral cats with similar home range sizes (Liberg
Despite the low-density population in Russellville, feral cats in this study displayed overlapping home ranges which contradicts previous studies that found mostly solitary cats at low densities (Genovesi et al. 1995, Fromont et al. 1998, Tennent and Downs 2008). The evidence provided by the positive relationship between home range overlap and the number of artificial food sources within areas shared by neighboring feral cats supports the hypothesis that sociality in this population is promoted by the clumped distribution of food resources (Bonanni et al. 2007). I do not have long-term abundance or density estimates for the feral cat population within Russellville, but another possibility for these observations is that cat densities were higher in years prior to this study and the population recently experienced a decline yet maintained their social behavior. In addition, the Schnabel method assumption of equal trappability among all cats was violated in this study as several cats observed in natural and urban locations were unsuccessfully trapped, so overall density was likely underestimated (Lancia 2005).

The population density estimate of feral cats in natural trapping locations was similar to that estimated in urban trapping locations which contradicts studies of feral cats in urban and rural locations. Prior research has identified higher feral cat abundances in urban and suburban areas relative to rural and natural areas because of ample supplemental food sources in more developed areas (Liberg et al. 2000, Tennent and Downs 2008, Horn et al. 2011). The most plausible explanation for this discrepancy is that exurban landscapes such as Russellville are heterogeneous combining natural and anthropogenic features within and around natural landscapes (Theobald 2004, Hansen et al. 2005). Therefore, feral cats inhabit natural areas for some portion of their range or for different seasons, but have the ability to utilize artificial food sources because of the
proximity of human residences to these natural areas. Of the 6 feral cats radiocollared in natural locations, 5 were observed in more anthropogenically modified habitats \( \geq 10 \) times during the course of tracking. For example, the 2 cats from natural areas that I included in compositional analyses of macrohabitat use had an average of 14\% of points located in open-low intensity developed areas and 11\% of points in medium-high intensity developed areas. The only cat originating in a natural area that was never observed spending time in modified habitats died 3 weeks after radiocollaring.

The greatest limitations in this assay of space use by feral cats was that the sample of cats was not representative of the cats in Russellville because only 2 cats that were captured in natural areas had sufficient radiotelemetry point locations to be included in home range and compositional analyses. In addition, feral cats in natural locations appeared to be trap-shy because I visually detected several cats in these areas that I was never able to trap. Ideally, I could have pre-baited traps in natural areas for extended periods of time to acclimate cats to entering the traps, but considering most natural areas were public parks, the risk of trap theft prevented this option.

**Management Recommendations**

Although the feral cat population in Russellville appears to be at a low density, their relatively large home range areas imply that each cat may influence its community over a large spatial scale. Alarmingly, feral cats infected with FeLV or FIV appear to use the same amount of space as uninfected cats, which increases the importance of a feral cat management plan in the city. In addition, infected cats used disproportionately more developed and pasture and hay field habitats than expected based on availability, which likely increases their opportunities for contact with pet cats and other feral cats,
especially around concentrated food sources. Trapping should occur in open-low and medium-high intensity developed areas as well as pasture and hay fields year-round.

**LITERATURE CITED**


Table 2.1. Population densities (cats/ha) and home range means (ha) for male and female domestic cats (*Felis catus*) from around the world (Liberg et al. 2000).

<table>
<thead>
<tr>
<th>Density</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;30</td>
<td>15.00 – 620.00</td>
<td>19.00 – 170.00</td>
</tr>
<tr>
<td>300-500</td>
<td>2.62 – 8.40</td>
<td>0.84 – 1.77</td>
</tr>
<tr>
<td>&gt;2,000</td>
<td>0.72 – 0.75</td>
<td>0.27 – 0.51</td>
</tr>
</tbody>
</table>
Table 2.2. Feral cat (*Felis catus*) annual and seasonal home range (ha; mean ± SE) for 95% minimum convex polygons (MCP), 95% kernel density estimates (KDE), and 50% kernel density estimates (core), and number of telemetry point locations (mean ± SE) for each home range estimate in Russellville, Arkansas 2012 – 2014. Different letters indicate significant differences ($P < 0.01$) between KDE, MCP, and core estimates for annual estimates or within a season.

<table>
<thead>
<tr>
<th>Home range estimate</th>
<th>Annual</th>
<th>Warm</th>
<th>Cold</th>
</tr>
</thead>
<tbody>
<tr>
<td>MCP</td>
<td>15.17 ± 3.55$^A$</td>
<td>9.03 ± 2.83$^A$</td>
<td>11.09 ± 2.14$^B$</td>
</tr>
<tr>
<td>KDE</td>
<td>19.76 ± 4.28$^A$</td>
<td>15.33 ± 4.37$^A$</td>
<td>23.91 ± 4.27$^A$</td>
</tr>
<tr>
<td>Core</td>
<td>3.73 ± 0.95$^C$</td>
<td>2.97 ± 0.99$^C$</td>
<td>5.09 ± 0.95$^C$</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>No. telemetry points</th>
<th>Annual</th>
<th>Warm</th>
<th>Cold</th>
</tr>
</thead>
<tbody>
<tr>
<td>MCP</td>
<td>97.06 ± 2.35</td>
<td>51.19 ± 1.82</td>
<td>45.86 ± 1.08</td>
</tr>
<tr>
<td>KDE and Core</td>
<td>102.17 ± 2.47</td>
<td>53.89 ± 1.92</td>
<td>48.28 ± 1.14</td>
</tr>
</tbody>
</table>
Table 2.3. Home range (mean ha ± SE) estimates of 95% minimum convex polygons (MCP), 95% kernel density estimates (KDE), 50% KDE estimates (Core) of male and female feral cats (*Felis catus*) in Russellville, Arkansas 2012 – 2014. Different letters indicate significant differences ($P < 0.05$) between the sexes.

<table>
<thead>
<tr>
<th>Sex</th>
<th>MCP</th>
<th>KDE</th>
<th>Core</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>22.14 ± 5.74$^A$</td>
<td>29.17 ± 7.17$^A$</td>
<td>5.83 ± 1.67$^A$</td>
</tr>
<tr>
<td>Female</td>
<td>9.60 ± 3.09$^B$</td>
<td>12.26 ± 2.90$^B$</td>
<td>2.04 ± 0.39$^B$</td>
</tr>
</tbody>
</table>
Table 2.4. Home range (mean ha ± SE) estimates of 95% minimum convex polygons (MCP), 95% kernel density estimates (KDE), 50% KDE estimates (Core) of feral cats (*Felis catus*) that tested positive for feline leukemia and/or feline immunodeficiency viruses and cats that tested negative for these viruses in Russellville, Arkansas 2012 – 2014. Home range differences between infected and uninfected cats were not significant (*P* < 0.05).

<table>
<thead>
<tr>
<th>Virus infection status</th>
<th>MCP</th>
<th>KDE</th>
<th>Core</th>
</tr>
</thead>
<tbody>
<tr>
<td>Infected</td>
<td>17.73 ± 9.32</td>
<td>23.4 ± 11.90</td>
<td>4.50 ± 2.45</td>
</tr>
<tr>
<td>Uninfected</td>
<td>14.19 ± 3.65</td>
<td>18.35 ± 4.15</td>
<td>3.43 ± 0.98</td>
</tr>
</tbody>
</table>
Table 2.5. Simplified ranking matrices for land cover use by feral cats (*Felis catus*) at the 2nd order scale in Russellville, Arkansas 2012 – 2014. Each matrix compares proportional habitat use as determined by the number of point locations per cat within each habitat relative to habitats available in 100% minimum convex polygon of all point locations for all cats. The (-/+) signs indicate the sign of the mean number in the matrix and triple signs indicate significant deviation from random (*P* < 0.05).

<table>
<thead>
<tr>
<th></th>
<th>Open-low</th>
<th>Med-high</th>
<th>Forest</th>
<th>Pasture &amp; hay field</th>
<th>Rank</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Annual</strong></td>
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<tr>
<td>Open-low</td>
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<td>Med-high</td>
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<td>Forest</td>
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<tr>
<td><strong>Warm</strong></td>
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<td>Open-low</td>
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<td>Med-high</td>
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<td>Forest</td>
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<tr>
<td>Pasture &amp; hay field</td>
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<tr>
<td><strong>Cold</strong></td>
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<tr>
<td>Med-high</td>
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<td>Pasture &amp; hay field</td>
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<td>3</td>
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Table 2.6. Simplified ranking matrices for 2\textsuperscript{nd} order habitat use by feral cats (*Felis catus*) that tested negative for feline leukemia virus and/or feline immunodeficiency virus and cats that were infected with these viruses in Russellville, Arkansas 2012 – 2014. Each matrix compares proportional habitat use as determined by the number of point locations per cat within each habitat relative to habitats available in 100% minimum convex polygon of all point locations for all cats. The (-/+) signs indicate the sign of the mean number in the matrix and triple signs indicate significant deviation from random (\(P < 0.05\)).

<table>
<thead>
<tr>
<th></th>
<th>Uninfected</th>
<th>Infected</th>
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<th>Uninfected</th>
<th>Infected</th>
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<tr>
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<td>Forest</td>
<td>Pasture &amp; hay field</td>
<td>Rank</td>
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<td>Open-low</td>
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<td>Pasture &amp; hay field</td>
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<td><strong>Warm</strong></td>
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<td>Open-low</td>
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<td>Pasture &amp; hay field</td>
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**Cold**

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<thead>
<tr>
<th></th>
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<tbody>
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<tr>
<td>Forest</td>
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<td>Pasture &amp; hay field</td>
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</tbody>
</table>
Table 2.7. Simplified ranking matrix for 3\textsuperscript{rd} order habitat use by feral cats (\textit{Felis catus}) in Russellville, Arkansas 2012 – 2014. The matrix compares proportional core (50\% kernel density estimate) habitat use as determined by the number of point locations per cat within each habitat relative to habitats available within its 95\% kernel density estimate. The (-/+\(+\)) signs indicate the sign of the mean number in the matrix and triple signs indicate significant deviation from random (\(P < 0.05\)).

<table>
<thead>
<tr>
<th></th>
<th>Open-low</th>
<th>Med-high</th>
<th>Forest</th>
<th>Pasture &amp; hay field</th>
<th>Rank</th>
</tr>
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<tbody>
<tr>
<td>Open-low</td>
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<td>+</td>
<td>+++</td>
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</tr>
<tr>
<td>Med-high</td>
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<td></td>
<td>+++</td>
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<tr>
<td>Forest</td>
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<td>4</td>
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<tr>
<td>Pasture &amp; hay field</td>
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<td></td>
<td>3</td>
</tr>
</tbody>
</table>
Figure 2.1. National Land Cover Database 2011 land cover, roads, and railroads in and around Russellville, Arkansas. Open-low intensity development includes developed open spaces with <25% impervious surfaces and low-intensity development with 20-49% impervious surfaces. Medium-high intensity development includes medium-intensity development with 50-79% impervious surfaces and high-intensity development with >80% impervious surfaces. “Other” includes barren land, shrub/scrub, grassland/herbaceous, cultivated croplands, and wetlands.
CHAPTER 3:
MICROHABITAT USE BY FERAL CATS IN AN EXURBAN AREA

Identification of a species’ habitat requirements is essential for wildlife management (Kolowski and Woolf 2002). Feral cats are mostly nocturnal and shelter availability within a given habitat, particularly DRSs that provide protection from weather and predators, may influence cat distribution and survival (Calhoon and Haspel 1989, Harper 2007, Horn et al. 2011). In other wild felids (e.g., bobcats, European wildcats [Felis silvestris silvestris], Canada lynx [Lynx canadensis] and Eurasian lynx [Lynx lynx]), DRSs are generally characterized by thick undergrowth and dense vegetation cover (Anderson 1990, Kolowski and Woolf 2002, Podgórski et al. 2008, Jerosch et al. 2010). However, DRS research for these species was conducted in relatively natural habitats (Anderson 1990, Kolowski and Woolf 2002, Podgórski et al. 2008, Jerosch et al. 2010) and I found no published research that examined DRSs in more anthropogenically-modified habitats.

To my knowledge, all research into feral cat DRSs has occurred in Australia and these studies made no attempt to relate DRS use with availability within specific habitats (Jones and Coman 1982, Barratt 1997, Norbury et al. 1998). For instance, Norbury et al. (1998) reported that feral cats in a wilderness area used 11.5 ± 3SD different DRSs within their home ranges. Although these authors collected measures of topography, vegetation density, and presence of surface rock, they did not collect data about the relative availability of habitat for DRSs. In addition, Norbury et al. (1998) found no statistical relationship regarding topography, vegetation density, or presence of surface rock and frequency of DRS use. Jones and Coman (1982) investigated home ranges and
population ecology of feral cats in a semi-arid national park and although they discussed favored DRSs observed during the study, they did not provide any empirical data concerning DRS observations. The DRSs reported in both of these studies included hollow trees or logs, dense thickets, rabbit (Oryctolagus spp.) warrens (Jones and Coman 1982), and rocky areas with shrub cover (Norbury et al. 1998). Barrat (1997) examined home ranges and macrohabitat use by free-roaming pet cats in suburban and rural Australia and reported that some cats spent their days hiding in vegetation, rabbit warrens, drainage systems, and in or under buildings. Similar to the aforementioned studies, Barrat (1997) did not provide information about the habitats surrounding DRSs and therefore analysis of DRS characteristics used by feral cats based on availability could not be conducted. Due to the paucity of information in the literature regarding feral cat DRS use and availability, a multivariate analysis is warranted.

Habitat characteristics associated with DRS use is understudied in feral cats, but is important for effective management because shelter availability may limit population size (Calhoon and Haspel 1989). Therefore, my goal was to characterize summer DRS use by feral cats via microhabitat and macrohabitat analyses in an exurban city. My main objective was to identify habitat characteristics that will allow managers to predict areas used by feral cats which will increase knowledge about feral cat ecology and provide valuable insight to better focus trapping effort in future research or management practices.

METHODS

Study Area

Please see the study area description in Chapter 1.
Capture and Handling

Please see the capture and handling methods in Chapter 1.

Radiotelemetry

Please see the radiotelemetry methods in Chapter 2.

DRS Use and Availability

I identified summer DRSs by homing in on individual cats once weekly for 15 consecutive weeks (12 May – 24 August 2013) between 1000 – 1600hr and conducted microhabitat sampling of 1 DRS for each cat weekly. To ensure data accurately reflected environmental conditions on a given day, I measured habitat variables upon locating the DRS and was therefore unable to avoid disturbing the cat. I also measured microhabitat variables at 1 random location of each radiocollared cat immediately following DRS measurements. I identified random locations by walking 50m from the DRS in 1 of 8 directions (north, south, east, west, northwest, northeast, southwest, and southeast), which I selected through a random number generator. If I was unable to use the selected direction (i.e., no access to private property or open water), I used the next direction on the list of random directions. At the random location, I selected the most likely resting site for a cat. For instance if the random location was a parked car, I measured variables under the car as opposed to on top of the car.

I collected the same microhabitat variables at the DRSs and random sites. Little is known about microhabitat use by feral cats, so I measured parameters identified as important for microhabitat selection by European wildcats: vegetation density and overhead cover (Jerosch et al. 2009). I used a density board to measure horizontal structure and vegetation density, which resulted in 6 measures of vegetation density (each
level was 0.305m tall and the 6\textsuperscript{th} level stopped at 1.83m above ground) for each location. I conducted a one-way ANOVA (PROC GLM, $\alpha = 0.05$ for all statistical analyses; SAS Institute, Cary, North Carolina 2010) with Tukey’s HSD (TUKEY in the MEANS statement) on vegetation density at feral cat DRSs and determined that levels 1 – 5 were not significantly different from one another (mean % level cover ranged 29.2 – 36.9), but were different from level 6 (mean % level cover was 27.5; $F_5 = 3.92 \; P = 0.002$). Therefore, I reduced the number of vegetation variables for all DRSs and random locations by calculating the mean vegetation density from levels 1 – 5. I used a spherical densiometer to measure overhead cover directly above the DRS or random location (Jerosch et al. 2009). If the cat was still at the DRS when I approached the entrance, I estimated the proportion of the cat visible (0\%, 25\%, 50\%, 75\%, 100\%) from a kneeling position 10m outside the DRS at the 4 cardinal directions to assess ground-level obscurity. At control locations or if the cat fled its DRS, I used a 30-cm round pillow placed into the DRS as a surrogate for a sleeping cat. Summers in Russellville are typically hot and dry so thermoregulation may be an important determinant of DRS use. Therefore, I measured the internal and external temperatures of DRSs and random locations. I also recorded length (cm), width (cm), and aspect of the largest entrance (if applicable) of the DRSs.

I used ArcGIS and NLCD (Jin et al. 2013) to identify the land cover type in which DRSs were located. I also used the NEAR feature to determine distance of DRSs and random locations to the nearest major and minor roads, permanent water (e.g., streams, ponds, and lakes that hold water year round), known feeding stations and refuse (dumpsters and trash containers), and patch edge of medium-high intensity development.
land cover (Delahunt 2011). In addition, I characterized DRS locations into 5 groups: vegetation; under anthropogenic structure; inside anthropogenic structure; underground; and in the open (Table 3.1).

From the micro-and macrohabitat data, I initially had 8 variables that may predict where a DRS was located (Table 3.2). I first examined all DRS and random locations to identify collinearity (PROC CORR) among the variables. Then I minimized collinearity and reduced the number of variables via cluster analysis (PROC VARCLUS). Cluster analysis is a multivariate process that partitions variables into mutually exclusive groups having high within-cluster correlation and little correlation among clusters (Urbanek and Nielsen 2013). Within each cluster, I identified the variable having the lowest $1 - R^2$ value as the variable that best represented its respective cluster (Urbanek and Nielsen 2013; Table 3.2). This procedure isolated 6 clusters that explained 97.01% of the variation within the data and thus I reduced the 8 original variables to 6.

Based on European wildcat habitat selection and field observations of feral cats, the broad factors that may explain feral cat DRS use are likely: predator avoidance, edge effects, food availability, and thermal regulation (Jerosch et al. 2008). I developed 13 a priori models focused on the 6 micro-and macrohabitat variables related to these broad factors (Table 3.3; Lesmeister et al. 2008). My study design of sampling multiple DRSs and random locations per cat was analogous to repeated measures. Generalized estimating equations (GEE) are an extension of generalized linear models that accounts for within-subject correlation among response variables and is applicable for analyzing data that are not normally distributed (Zeger et al. 1988, Ballinger 2004). The GEE procedure calculates Pan’s quasilikelihood under the independence model information
criterion (QIC) which is assessed similar to Akaike’s information criterion (AIC; see Chapter 1) to select the most parsimonious model within a model set (Ballinger 2004). Whereas QIC is used only to identify a correlation structure, the modified QIC_u provides a comparison of models with the same quasi-likelihood form and same correlation matrix by adjusting for the different number of covariates between models (Ekstrom and Ekstrom 2012) and was therefore a more appropriate estimate to identify competing models. Given that GEE is an estimating procedure and there is no likelihood function, likelihood-ratio tests for assessing model fit are not available in standard statistics packages (Zorn 2001, Ballinger 2004). I used the QIC_u generated from GEE and logistic regression (PROC GENMOD, REPEATED subject = cat) to identify which micro- and macrohabitat variables (Table 3.2) affected 4th order site (DRS) use by feral cats (SAS Institute Inc. 2014). I considered models with ≤2 ΔQIC_u values from the most parsimonious model as supported (Zeger et al. 1988). Then, I used the standardized parameters and Quasilikelihood weights for each model ≤2 ΔQIC_u values from the most parsimonious model to create a composite model. In addition, I calculated the Quasilikelihood relative importance weights (ω) for each variable within the composite model (Anderson 2008).

Models regarding predator avoidance (n = 3) included vegetation density around the DRS and visual obscurity of the cat within (Tables 3.2 and 3.3). An important strategy for feral cat survival is remaining undetected by predators while resting or caring for young. Therefore, factors with potential positive effects on site use may include high vegetation density and visual obscurity to protect cats from predators. In urban areas where vegetation density may be low, anthropogenic structures (i.e., culverts or
buildings) may still provide high levels of visual obscurity.

Edge effect models \((n = 3)\) included spatial proximity to roads and medium-high intensity development land cover patches (Tables 3.2 and 3.3). Avoidance of contact with humans may contribute to the nocturnal behavior of feral cats (Horn et al. 2011). Thus, automobile and foot traffic may stress feral cats and deter a cat from using an area as a DRS.

Food availability models \((n = 2)\) included spatial proximity to medium-high intensity development and permanent water (Tables 3.1 and 3.2). The availability of food subsidies is positively correlated with development intensity because areas of medium-high intensity development have higher concentrations of restaurant dumpsters, feral cat feeding stations, and domiciles with doorstep food for free-roaming pet cats than less developed areas. Considering this relationship between food availability and development, I categorized the model containing just proximity to medium-high intensity development as edge effects and food availability. Hot, dry summers in Russellville are likely stressful times for feral cats and cats may benefit from close proximity to artificial food and permanent water sources which will limit time spent foraging.

Given the typical summer weather in Russellville, keeping cool and well hydrated is important for cats. Thermal regulation models \((n = 7)\) included overhead cover, proximity to permanent water, and the difference between temperature inside and outside of the DRS (Tables 3.1 and 3.2). Shaded sites will remain cooler throughout the day than sites in full sun, thus higher overhead cover may positively influence a cat to use an area for a DRS. Also, the further a DRS is from permanent water, the more time that cat will spend traveling to stay hydrated, so proximity to permanent water may contribute to a
cat’s use of a DRS. The predator avoidance model containing just the variable overhead cover could also be considered a thermal regulation model because high overhead cover provides shade, so I categorized this model as predator avoidance and thermal regulation. In addition, the food availability model containing proximity to water may also relate to thermal regulation, so I categorized this model as food availability and thermal regulation.

RESULTS

I identified 319 summer DRSs used by 24 feral cats (11 females, 13 males; \( \bar{x} \pm SE \) throughout: 13.3 ± 0.72 locations/cat). Five of the 29 radiocollared cats that were monitored for survival and home range analyses (Chapters 1 and 2, respectively) disappeared from the study area \((n = 2)\) or died \((n = 3)\) before DRS identification began. Nineteen of the cats were captured in urban locations and 5 in natural locations, but 1 cat captured in a natural location moved to an urban location shortly after capture, which is where I located all of his DRSs. I found only 1 cat in most DRSs, excluding females with kittens, but did observe DRS sharing (≥2 cats resting <2m of one another) on 7 separate occasions: 2 intact males shared DRSs on 2 occasions; a male resting with an unmarked pregnant female on 1 occasion; a female with her 4 kittens resting with an unmarked male on 1 occasion and with another marked male on a different occasion; and 2 separate occasions of a marked female resting with a marked male. All of the observed DRS sharing in this study occurred <165m (mean ± SE = 112.89 ± 21.56) of known artificial food sources.

Feral cats used DRSs broadly categorized as vegetation (39.8%) the most frequently (Table 3.1). Twenty-one cats (6.05 ± 0.96 DRSs/cat) were observed using
vegetated DRSs and most of these DRSs were within thick herbaceous or woody growth (74.0%) and located in the open-low intensity development areas (53.5%; Table 3.4). Daytime resting sites categorized as under structure comprised 32.3% of DRSs and were also used by 21 feral cats (4.91 ± 0.82 DRSs/cat); 65.0% of which were underneath a house, shed, mobile home, or industrial shipping container. The most common land cover type containing under-structure DRSs was also open-low intensity development (48.5%). Resting sites categorized as inside structure (15% of DRSs) were used by 13 feral cats (3.69 ± 0.90 DRSs/cat). Within this category, cats most often (70.8%) used the inside of sheds, garages, and barns and many (37.5%) of the DRSs inside structures were located in the pasture and hay field land cover type. The underground category comprised 8.15% of DRSs and was used by 10 cats (2.60 ± 0.78 DRSs/cat). Half (50.0%) of all underground DRSs were located inside storm drains and 84.6% were within open-low intensity developed land cover. The least used (4.70%) category of DRSs was open with no protective cover and I observed 9 feral cats using these sites (1.67 ± 0.29 DRSs/cat). Open DRS use by feral cats was equally split (33.3% each) between sites in parking lots or walkways and cats perched on top of objects (i.e., garbage can or chair). Open DRSs were most often (66.7%) located in open-low intensity developed land cover.

Of the NLCD cover types, the open-low intensity development was used most often by feral cats (51.7% of DRS locations; n = 22 cats; 7.50 ± 1.08 DRSs/cat; Table 3.4), followed by medium-high intensity development (29.1%; n = 17 cats; 6.47 ± 0.93 DRSs/cat), pasture and hay fields (16.6%; n = 9 cats; 5.89 ± 1.86 DRSs/cat), and forest habitat (2.51%; n =3 cats; 2.67 ± 1.20 DRSs/cat). Within the different land cover types,
feral cats used DRSs within the broad categories differently ($G_{12} = 40.45 P < 0.001$).

Feral cats utilizing DRSs within open-low intensity development used underground DRSs more than expected and DRSs located inside structures less than expected (Table 3.4).

Feral cats with DRSs located in medium-high intensity development used under structures more than expected and underground DRSs less than expected. In pasture and hay fields, cats used DRSs inside structures more than expected and underground DRSs less than expected. I made few observations of feral cats using forest land cover for DRSs, but those cats used inside structures less than expected and open areas more than expected. Seventeen cats ($3.12 \pm 0.74$ DRSs/cat) used 53 DRSs that had $>1$ entrance. The entrance perimeters ranged from $60.00 – 1,072.32$ cm ($217.83 \pm 23.28$ cm) and most faced south ($n = 27$), followed by north ($n = 9$), east ($n = 9$), and west ($n = 8$).

I identified 2 competing models that explained 82% of the Pan’s quasilikelihood under the independence model criterion model weights (Table 3.3). Internal and external DRS temperature difference and overhead cover had the strongest effects on DRS use by feral cats and were included in both competing models (Quasilikelihood relative importance weight: $\omega = 0.82$ for each variable). These results indicate that DRS locations with lower temperature inside relative to directly outside the DRSs and areas with high overhead cover were used frequently by feral cats. Given that ground-level visual obscurity was highly correlated with overhead cover ($r = 0.79 P < 0.001$), I can assume that cats frequently use DRS with more ground-level visual obscurity than open areas. The second model included proximity to water and indicated that DRS use increased slightly as distance of DRS from water decreased. However, the extremely low parameter estimate and the low relative importance weight ($\omega = 0.25$) indicates that this
variable does not contribute as much as the previously stated variables to DRS use by feral cats.

**DISCUSSION**

To my knowledge, characteristics that influence daytime resting sites by feral cats have never been published. My objective was to characterize summer DRS use by exurban feral cats by way of macro- and microhabitat analyses to aid targeted trapping of feral cats for management. The most frequently used summer DRSs by feral cats in this study were in thick herbaceous or woody vegetated areas, followed by DRSs located under anthropogenic structures. Most DRSs were located within the open-low intensity developed areas of the city. The 4th order habitat use model indicated that the most important factors contributing to DRS use were the difference in temperature inside relative to outside of the DRS, high overhead cover, and high ground-level visual obscurity of the cat.

I observed DRS sharing mostly between a single male cat and a single female, but also observed DRS sharing between 2 male feral cats and between a female cat, her litter of kittens, and ≥2 different male cats. The frequency with which feral cats shared DRSs with other cats in this study was unexpected because cats are typically solitary when they live in low-density populations (Genovesi et al. 1995, Fromont et al. 1998, Tennent and Downs 2008). This behavior of being tolerant of other cats is more characteristic of feral cats living at densities >20 cats/ha (Genovesi et al. 1995, Liberg et al. 2000). However, given that all observed DRS sharing occurred near known artificial food, these clumped food resources within Russellville likely promote sociality in this population despite the relatively low population density observed (Bonanni et al. 2007).
Although Calhoon and Haspel (1989) suggested that shelter availability may be a factor that limits feral cat abundance, the variety of DRSs utilized by feral cats in this study and their ability to maneuver into small spaces conflicts with that claim. While most feral cats used DRSs in thick vegetation or under anthropogenic structures, I also observed cats utilizing the inside of anthropogenic structures, underground openings, and open areas with no protective cover. These observations are consistent with findings from feral cat research in Australia in which feral cats utilized vegetation, rabbit warrens, drainage systems, and in or under buildings as DRSs (Barratt 1997).

The majority of DRSs were located in open-low intensity development and use of this land cover type was observed slightly more frequently than expected. Medium-high intensity developments were used half as often as open-low intensity, followed by pasture and hay fields, and then forests used least of all; these results agree with areas of core home range use of the cats in this study (Chapter 2). These observations may result from the uneven sample with the majority of cats used in DRS analyses having been captured in urban locations. However, 1 male feral cat captured in an urban location used pasture and hay fields for all observed DRSs, but another male cat captured in a natural location mostly used open-low and medium-high intensity developments for DRSs. Therefore, DRS use may reflect individual personalities of different feral cats as well as differences in habitat availability.

Analysis of 4th order summer habitat use indicated that feral cats used DRSs that provided temperatures cooler than the ambient temperature and overhead- and ground-level visual obscurity. These factors are important for survival because they provide thermoregulation and protection from predators, but they did not appear to be strong
predictors of DRS use in the composite model. Although vegetation was the most frequently used DRS type, density of vegetation did not influence models of DRS use. This result is likely because feral cats could gain the same levels of protection and thermoregulation in non-vegetated areas by utilizing anthropogenic structures. Therefore, my objective to identify habitat characteristics that would facilitate prediction of likely feral cat DRSs was unsuccessful.

The major limitation in my DRS use analyses was that the sample was skewed towards cats living in urban areas. By summer 2013 when I conducted DRS sampling, all but 2 feral cats living in natural areas had disappeared or died and this small sample prevented valid statistical analysis to determine if DRS use differed between urban and natural sites. In addition, time constraints limited identifying DRSs outside of the summer months, so it is unclear whether DRS use observed in this study shifts to different microhabitats during other seasons. Given that winter vegetation is sparser and may not provide sufficient cover, future research on seasonal DRS use is warranted.

Management Recommendations

Given the variety of DRSs used by feral cats in Russellville, managers may have difficulty identifying trapping locations that would increase the efficiency of capturing feral cats in low-density cat populations. The inability to accurately predict the microhabitat used by feral cats means that control attempts will likely require intensive effort (Chapter 1). In addition, the lower the density of a cat population, the larger the feral cat home ranges (Liberg et al. 2000). In turn, trap encounter rates by cats may be low which would increase the difficulty of controlling the population by way of trapping for neutering and/or removal. More research on Russellville’s feral cat population,
particularly annual and seasonal DRS use and DRS use by feral cats inhabiting natural areas is warranted.

Based on 2nd and 3rd order habitat use of cats in Russellville (Chapter 2) and the types of DRSs most frequently observed within these habitats, managers should concentrate feral cat trapping efforts in and around heavily vegetated areas in open-low and medium-high intensity developments and in locations where cats can access underneath buildings, mobile homes, and industrial shipping containers that provide cool temperatures and ample cover during the summer. Feral cats in urban areas will likely be easier to trap because they are accustomed to maneuvering around anthropogenic objects and utilizing artificial food sources (Chapter 2).

Because feral cats in open-low and medium-high intensity developed areas most frequently used thick vegetation for DRSs, managers may work to limit availability of these sites by mowing or bush hogging undeveloped lots to prevent thick herbaceous or woody growth within the developed land cover areas. In addition, encouraging the public to use barriers (e.g., skirting, lattice, chicken wire) around raised anthropogenic structures would prevent feral cats utilizing these areas as DRSs and dens. Unfortunately, limiting access into anthropogenic structures and underground areas may be more difficult to implement.

**LITERATURE CITED**


Table 3.1. Broad categories of exurban feral cat (*Felis catus*) daytime resting sites (DRSs; *n* = 319) with descriptions and relative frequency of use (%) in Russellville, Arkansas, 2013.

<table>
<thead>
<tr>
<th>DRS category and description</th>
<th>Use</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Vegetation (n = 127)</strong></td>
<td></td>
</tr>
<tr>
<td>Within thick herbaceous or woody growth</td>
<td>74.02</td>
</tr>
<tr>
<td>In flower bed or under shrub</td>
<td>11.02</td>
</tr>
<tr>
<td>Within vegetation of brush row or fence row</td>
<td>9.45</td>
</tr>
<tr>
<td>At base of tree or within exposed roots</td>
<td>2.36</td>
</tr>
<tr>
<td>On tree limb</td>
<td>1.57</td>
</tr>
<tr>
<td>In woods with fairly open understory</td>
<td>1.57</td>
</tr>
<tr>
<td><strong>Under structure (n = 103)</strong></td>
<td></td>
</tr>
<tr>
<td>Under house, shed, mobile home, or commercial shipping container</td>
<td>65.05</td>
</tr>
<tr>
<td>On ground under vehicle</td>
<td>17.48</td>
</tr>
<tr>
<td>Under rubbish heap</td>
<td>13.59</td>
</tr>
<tr>
<td>Under dumpster</td>
<td>3.88</td>
</tr>
<tr>
<td><strong>Inside structure (n = 48)</strong></td>
<td></td>
</tr>
<tr>
<td>Inside shed, garage, or barn</td>
<td>70.83</td>
</tr>
<tr>
<td>On porch or doorstep enclosed on $\geq$ 2 sides</td>
<td>22.92</td>
</tr>
<tr>
<td>Within undercarriage of vehicle</td>
<td>4.17</td>
</tr>
<tr>
<td>Inside man-made log pile</td>
<td>2.08</td>
</tr>
<tr>
<td><strong>Underground (n = 26)</strong></td>
<td></td>
</tr>
<tr>
<td>Location</td>
<td>Percentage</td>
</tr>
<tr>
<td>----------------------------------------</td>
<td>------------</td>
</tr>
<tr>
<td>In storm drain</td>
<td>50.00</td>
</tr>
<tr>
<td>In culvert</td>
<td>34.62</td>
</tr>
<tr>
<td>In underground cavity</td>
<td>15.38</td>
</tr>
<tr>
<td><strong>Open</strong> ($n=15$)</td>
<td></td>
</tr>
<tr>
<td>On ground in parking lot or on walkway</td>
<td>33.33</td>
</tr>
<tr>
<td>Perched on object (i.e., garbage can, chair)</td>
<td>33.33</td>
</tr>
<tr>
<td>On mowed lawn</td>
<td>26.67</td>
</tr>
<tr>
<td>On bare ground</td>
<td>6.67</td>
</tr>
<tr>
<td><strong>Total</strong> ($n=319$)</td>
<td></td>
</tr>
</tbody>
</table>
Table 3.2. Abbreviations (Abbrev), descriptions, and cluster analysis results of variables collected at exurban feral cat (*Felis catus*) daytime resting sites and random locations in Russellville, Arkansas, 2013. An asterisk (*) after the variable abbreviation identifies variables that represented the clusters used in a priori repeated measures logistic regression models to examine habitat use (Table 3.3).

<table>
<thead>
<tr>
<th>Abbrev</th>
<th>Description</th>
<th>1-(R^2) ratio</th>
<th>Cluster</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cov*</td>
<td>Overhead cover (%)</td>
<td>0.1265</td>
<td>1</td>
</tr>
<tr>
<td>Vis</td>
<td>Ground level visual obscurity of cat (%)</td>
<td>0.1330</td>
<td>1</td>
</tr>
<tr>
<td>Dev*</td>
<td>Proximity to medium-high intensity development (m)</td>
<td>0.0137</td>
<td>2</td>
</tr>
<tr>
<td>Food</td>
<td>Proximity to known food subsidies (m)</td>
<td>0.0138</td>
<td>2</td>
</tr>
<tr>
<td>Wat*</td>
<td>Proximity to permanent water (m)</td>
<td>0.0000</td>
<td>3</td>
</tr>
<tr>
<td>Temp*</td>
<td>Temperature difference (external minus internal °C)</td>
<td>0.0000</td>
<td>4</td>
</tr>
<tr>
<td>Road*</td>
<td>Proximity to roads (m)</td>
<td>0.0000</td>
<td>5</td>
</tr>
<tr>
<td>Veg*</td>
<td>Vegetation density (%)</td>
<td>0.0000</td>
<td>6</td>
</tr>
</tbody>
</table>
Table 3.3. Broad factor model categories and associated a priori repeated measure logistic regression models for assessing daytime resting site use by exurban feral cats (*Felis catus*) in Russellville, Arkansas, 2013. Table includes standardized parameter estimates and standard error, the number of parameters (*K*), Pan’s quasilikelihood under the independence model information criterion (QICₚ), distance from the lowest QICₚ values (ΔQICₚ), and the quasilikelihood model weights (*ω*) used to evaluate models.

Descriptions of variables are in Table 3.2.

<table>
<thead>
<tr>
<th>Category</th>
<th>Model</th>
<th><em>K</em></th>
<th>QICₚ</th>
<th>ΔQICₚ</th>
<th><em>ω</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Thermal Regulation</td>
<td>-6.01±0.59(Intercept) + 0.09±0.03(Temp) + 0.07±0.01(Cov)</td>
<td>3</td>
<td>453.20</td>
<td>0.00</td>
<td>0.57</td>
</tr>
<tr>
<td></td>
<td>-6.12±0.59(Intercept) + 0.09±0.03(Temp) + 0.07±0.01(Cov) + 0.00±0.00(Wat)</td>
<td>4</td>
<td>454.85</td>
<td>1.66</td>
<td>0.25</td>
</tr>
<tr>
<td></td>
<td>-5.91±0.68(Intercept) + 0.11±0.03(Temp) ± 0.07±0.01(Cov) + 0.01±0.00(Veg) - 0.01±0.00(Road) + 0.00±0.00(Dev) + 0.00±0.00(Wat)</td>
<td>7</td>
<td>455.54</td>
<td>2.35</td>
<td>0.18</td>
</tr>
<tr>
<td>Global</td>
<td>-6.09±0.64(Intercept) + 0.08±0.01(Cov)</td>
<td>2</td>
<td>465.32</td>
<td>12.13</td>
<td>0.00</td>
</tr>
<tr>
<td>Predator Avoidance &amp; Thermal Regulation</td>
<td>-6.17±0.69(Intercept) + 0.08±0.01(Cov) + 0.00±0.00(Veg)</td>
<td>3</td>
<td>466.39</td>
<td>13.20</td>
<td>0.00</td>
</tr>
<tr>
<td>Predator Avoidance</td>
<td>-6.15±0.65(Intercept) + 0.08±0.01(Cov) + 0.00±0.00(Wat)</td>
<td>3</td>
<td>467.21</td>
<td>14.01</td>
<td>0.00</td>
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<tr>
<td>Thermaral Regulation</td>
<td>-0.46±0.08(Intercept) + 0.14±0.02(Temp)</td>
<td>2</td>
<td>782.96</td>
<td>329.76</td>
<td>0.00</td>
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<tr>
<td>Predator Avoidance</td>
<td>0.00±0.00(Intercept) + 0.00±0.00(Veg)</td>
<td>2</td>
<td>887.44</td>
<td>434.25</td>
<td>0.00</td>
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<tr>
<td>Model Description</td>
<td>Formula</td>
<td>DF</td>
<td>$\chi^2$</td>
<td>$df$</td>
<td>$p$</td>
</tr>
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<td>---------------------------------------</td>
<td>-------------------------------------------------------------------------</td>
<td>----</td>
<td>----------</td>
<td>------</td>
<td>------</td>
</tr>
<tr>
<td>Edge Effect</td>
<td>$0.00 \pm 0.00 (\text{Intercept}) + 0.00 \pm 0.00 (\text{Road})$</td>
<td>2</td>
<td>888.42</td>
<td>435.22</td>
<td>0.00</td>
</tr>
<tr>
<td>Food Availability &amp; Thermal Regulation</td>
<td>$0.00 \pm 0.00 (\text{Intercept}) + 0.00 \pm 0.00 (\text{Wat})$</td>
<td>2</td>
<td>888.46</td>
<td>435.26</td>
<td>0.00</td>
</tr>
<tr>
<td>Edge Effect &amp; Food Availability</td>
<td>$0.00 \pm 0.00 (\text{Intercept}) + 0.00 \pm 0.00 (\text{Dev})$</td>
<td>2</td>
<td>888.46</td>
<td>435.26</td>
<td>0.00</td>
</tr>
<tr>
<td>Edge Effect</td>
<td>$0.00 \pm 0.00 (\text{Intercept}) + 0.00 \pm 0.00 (\text{Dev}) + 0.00 \pm 0.00 (\text{Road})$</td>
<td>3</td>
<td>890.42</td>
<td>437.22</td>
<td>0.00</td>
</tr>
<tr>
<td>Food Availability &amp; Thermal Regulation</td>
<td>$0.00 \pm 0.00 (\text{Intercept}) + 0.00 \pm 0.00 (\text{Dev}) + 0.00 \pm 0.00 (\text{Wat})$</td>
<td>3</td>
<td>890.46</td>
<td>437.26</td>
<td>0.00</td>
</tr>
<tr>
<td>Composite model</td>
<td>$-6.04 \pm 0.01 (\text{Intercept}) + 0.09 \pm 0.00 (\text{Temp}) + 0.07 \pm 0.00 (\text{Cov}) + 0.00 \pm 0.00 (\text{Wat})$</td>
<td>4</td>
<td>890.46</td>
<td>437.26</td>
<td>0.00</td>
</tr>
</tbody>
</table>
Table 3.4. Observed and expected frequency of daytime resting site (DRS) use by exurban feral cats (*Felis catus*) for each category of DRSs within each land cover type in Russellville, Arkansas, 2013. An asterisk (*) before the observed value indicates significance from the expected value (*P* < 0.05; *G*-test).

<table>
<thead>
<tr>
<th>DRS category</th>
<th>Med-high intensity development</th>
<th>Open-low intensity development</th>
<th>Pasture and hay field</th>
<th>Forest</th>
<th>Total observed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
<td>Observed</td>
<td>Expected</td>
<td>Observed</td>
</tr>
<tr>
<td>Vegetation</td>
<td>33</td>
<td>37.00</td>
<td>68</td>
<td>65.70</td>
<td>22</td>
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<tr>
<td>Under structure</td>
<td>*38</td>
<td>7.60</td>
<td>50</td>
<td>53.30</td>
<td>12</td>
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<tr>
<td>Inside structure</td>
<td>15</td>
<td>14.00</td>
<td>*15</td>
<td>24.80</td>
<td>*18</td>
</tr>
<tr>
<td>Underground</td>
<td>*4</td>
<td>7.60</td>
<td>*22</td>
<td>13.40</td>
<td>*0</td>
</tr>
<tr>
<td>Open</td>
<td>3</td>
<td>4.40</td>
<td>10</td>
<td>7.80</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>93</td>
<td>165</td>
<td>53</td>
<td>8</td>
<td>319</td>
</tr>
</tbody>
</table>