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LAND-USE PATTERNS AND POPULATION CHARACTERISTICS OF WHITE-TAILED DEER IN AN AGRO-FOREST ECOSYSTEM IN SOUTH CENTRAL MICHIGAN

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LAND-USE PATTERNS AND POPULATION CHARACTERISTICS OF WHITE-TAILED DEER IN AN AGRO-FOREST ECOSYSTEM IN SOUTH CENTRAL MICHIGAN

By

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ABSTRACT

LAND-USE PATTERNS AND POPULATION CHARACTERISTICS OF WHITE-TAILED DEER IN AN AGRO-FOREST ECOSYSTEM IN SOUTH CENTRAL MICHIGAN

By

Tim L. Hiller

Assessments of demographics and space use are important for habitat and harvest management of white-tailed deer (*Odocoileus virginianus*). These population characteristics often vary across a landscape, and by age (e.g., fawn, yearling, adult) and sex class. Knowledge of demographics and space use of young fawns is particularly limited, despite the potential for recruitment having a relatively large influence on deer population dynamics. My objectives were to describe age-specific survival, cause-specific mortality, and space use in an agro-forest ecosystem undergoing increasing urbanization (i.e., increasing housing developments, increasing human population) in south central Michigan. I captured, radiomarked, and monitored 66 deer during winter and 34 neonates during spring 2004–2006. Annual survival varied by age class (fawn = 0.51, yearling = 0.94, adult = 0.56), and annually based sources of mortality were primarily vehicle collisions (fawns) and hunter-harvest (adults). Two- and 6-month post-capture survival estimates of neonates were 81% and 67%, respectively, and canids caused most mortalities during both time periods. Yearlings had larger seasonal home ranges (agricultural growing season: $\bar{x} = 201.8$ ha ± 91.1 SE; non-growing season: $\bar{x} = 156.9$ ha ± 28.2 SE) than either fawns (60.2 ha ± 14.1; 116.3 ha ± 20.6) or adults (77.5 ha ± 9.6; 140.4 ha ± 23.4). Home ranges for fawns 0–2 months old averaged 40.9 ha (range = 2.7–166.8), with conifers and lowland deciduous forests selected in proportions higher than available on the study area. Adult female deer had relatively small home ranges compared to deer in other Michigan studies indicating that their habitat components were readily available. Additionally, this sex-age class is of primary interest to managers desiring to reduce high deer numbers. To describe cover selection of adult female white-tailed deer (*n* = 20), I used a multi-scale approach by varying definitions of cover use and availability. The number of cover types assigned as selected decreased from coarse (landscape) to fine (within home range) scales. Two cover types (conifers, upland deciduous forests) were consistently ranked as the most important regardless of scale. I used the concept of usable space (i.e., "ideal" permanent cover situations) to describe a potentially more accurate biological representation (compared to traditional home-range estimators) of space use by adult female white-tailed deer. Fixed-kernel home-range estimates might misrepresent space use by including cover types with no location estimates (i.e., no evidence of use). Usable space estimates (ha) were approximately 75% that of kernel home ranges, and were dominated (~87% of area) by upland deciduous forest, lowland shrub, agriculture, and coniferous cover types. Under the assumption that deer densities are positively correlated with the amount of usable space, several cover conversion scenarios (i.e., habitat manipulation) would theoretically change deer abundance on an area of interest by changing the amount of usable space. Knowledge of age-specific deer demographics and addressing deer-habitat management issues through a multi-scale perspective and a usable-space approach are both relatively recent but seemingly useful concepts that also have relevance to population ecology of deer and other wildlife species.

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ORGANIZATION OF DISSERTATION

This dissertation is organized into 5 chapters and 2 appendices that generally follow formatting guidelines for manuscripts submitted to *The Journal of Wildlife Management*; chapters 1–4 were formatted as complete manuscripts, so redundancy may occur (e.g., study area description) among these chapters. Chapter 1 provides general results on survival, cause-specific mortality, and space use of white-tailed deer. Chapter 2 provides similar information, but for white-tailed deer fawns for the time period from capture to 2 months old. Chapter 3 describes a multi-scale approach to assess resource selection of adult female white-tailed deer. Chapter 4 builds on Chapter 3 through space-use assessments and their direct applicability to habitat management in an increasingly urbanizing area. Finally, Chapter 5 provides an overview of conclusions based on previous chapters. Appendix A provides an assessment of location-estimate precision based on telemetry data, and Appendix B provides general identification and capture information on white-tailed deer from this study.

INTRODUCTION

White-tailed deer (*Odocoileus virginianus*) may be described as a ubiquitous species, inhabiting numerous vegetation types (e.g., Rolling Plains of Texas, coniferous-hardwood forests of Michigan's Upper Peninsula) and distributed throughout most of North and Central America (Baker 1984). It would seem logical that population characteristics (e.g., demographics, resource selection, space use) could shift substantially under differing landscape conditions. These characteristics must be scientifically evaluated for effective management of deer populations and their associated habitat.

Movements and demographics (e.g., annual survival estimates) of deer often vary throughout their distribution, and consequently should be measured at an appropriate scale (e.g., landscape) or scales for effective management. For example, research in the United States has shown annual home-range-size estimates ranged from 59 to 740 ha for nonmigratory deer (Marchinton and Hirth 1984:table 20; Pusateri 2003). Generally, home ranges of deer may increase in size from south to north due to climate (Severinghaus and Cheatum 1956), and home ranges are usually larger in more open vegetation (i.e., sparse vegetation; Marchinton and Hirth 1984).

Higher population densities in mammals may also result in smaller home ranges (Sanderson 1966), presumably as a response to maintain spacing among individuals for increasingly limited resources. In addition, the spatial distribution of an animal is influenced to some degree by the distribution of forage and predators within the animal's environment (Stephens and Krebs 1986:161–168). The multiple influences on size of home ranges of deer suggest that research and management considerations only at the landscape scale might not be as beneficial as management decisions based on studies considering >1 spatial scale. For example, habitat manipulation is one tool for wildlife management and as previously discussed, deer can use a wide variety of habitat conditions, so understanding the types and quantities of resources selected by deer at multiple scales should help us understand potential population responses to changes in habitat conditions.

Research at the state level has supported my assertions about space-use dynamics. Home ranges in Michigan's Upper Peninsula have been estimated at 730–1,859 ha (winter) and 1,255–3,037 ha (summer) for migratory deer (95% adaptive kernel; Van Deelen 1995), while in the northern Lower Peninsula, home ranges of migratory deer varied 202–354 ha (winter) and 329–337 ha (summer; 95% harmonic mean; Sitar 1996). Nonmigratory deer in the southwestern Lower Peninsula of Michigan had an estimated annual home range size of 50–740 ha (95% fixed kernel; Pusateri 2003). Resource selection among these study areas must also differ to some degree due to different ecosystem conditions and weather patterns.

Demographics are also important to estimate for wildlife management. Survival estimates are a key parameter when building population models to be used for wildlife management (White and Lubow 2002), as these estimates can describe the growth potential of a population. Studies in Michigan have included survival estimates of 22% (males) and 77% (females; Van Deelen 1995), a range of 53–71% (pooled by sex; Sitar 1996), and 40%–58% (pooled by sex; Pusateri 2003) annual survival for adults. Although some variation may exist among studies due to survival-estimation method (Mayfield for the former 2, Kaplan-Meier for the latter), generally, survival would seem to decrease with increasing latitude due in part to stochastic winter-weather events.

Potentially higher estimated neonate survival might be associated with areas of increasing land-use activities (e.g., agriculture, urban development), although survival will likely reach an asymptote or decline at some point of land-use activity. Within the United States, neonate survival (180 days post-capture) has been estimated at 47% (early urban development) and 96% (post-urban development, Florida Key neonates; Peterson et al. 2004), 46% and 59% (forested and agricultural areas, respectively, in Pennsylvania; Vreeland et al. 2004), 73% (agricultural, Iowa; Huegel et al. 1985), and 40% (forests and forest-agriculture borders, New Brunswick; Ballard et al. 1999). In Oklahoma, 90% of neonates died within 3 months of capture (prairie and woodland; Bartush and Lewis 1981). Fawn survival from capture as neonates to 220 days post-capture has been estimated at >76% within Michigan (southwestern Lower Peninsula; Pusateri Burroughs et al. 2006). In a suburban Chicago, Illinois forest preserve, fawn mortality was estimated to be as high as 95% (Piccolo 2002). Different survival estimates are likely complicated by differing habitat conditions used by deer throughout their distribution. This suggests the importance of understanding the relationship between population demographics and habitat when making management decisions.

OBJECTIVES

My goal was to make my findings applicable and usable for deer management within south central Michigan and other areas experiencing increasing land-use activities, such as urbanization. Specifically, my objectives were to

1. Estimate age-specific survival, cause-specific mortality, and space use of female white-tailed deer,

2. Estimate survival, cause-specific mortality, and space use of young fawns from time of capture (<2 weeks old) to 2 and 6 months post-capture,
3. Describe resource selection of adult female deer across multiple spatial scales,
4. Quantify and compare space use of adult female deer using two analytical methods (fixed-kernel and usable space), and
5. Estimate cover conversions, based on the concept of usable space, which will theoretically affect deer abundance on the study area.

My objectives were met by capturing and radiomarking multiple age classes of primarily female white-tailed deer within Jackson and Washtenaw counties during 2004–2006. Deer were monitored using telemetry techniques during this period. Michigan State University's All-University Committee on Animal Use and Care approved all capturing and handling procedures for my study (Application No. 01/04-006-00).

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CHAPTER 1

Age-specific Population Characteristics of White-tailed Deer in Southern Michigan

Age-specific Population Characteristics of White-tailed Deer in Southern Michigan

INTRODUCTION

Regulated harvest and habitat management for game species are 2 primary management methods used by state wildlife agencies. Consequently, accurate descriptions of population characteristics of game species such as estimates of age-specific demographics and space use are imperative during the decision-making process. Many factors influence survival and cause-specific mortality of cervids, including annual weather patterns (e.g., DelGiudice et al. 2006), predator-prey dynamics (e.g., Labisky and Boulay 1998), and the effects of hunter-harvest (e.g., Bender et al. 2000). A discussion of the effects of harvest on game species populations often involves additive versus compensatory effects of hunting on mortality, especially as the relative abundance of a species varies. Survival and other age-specific demographic estimates are important parameters for managers using simulation modeling to predict species abundance.

Knowledge of space use is relevant for managers to understand the importance of landscape features to a species. Spatial or temporal changes in cover may affect species abundance and age and sex structure, and potential future land-use changes (e.g., land ownership) may impact a state agency's ability to manage natural resources. Knowledge of relationships between space use and demographics is also important, as population characteristics often vary spatially and temporally across the landscape. For example, lower survival may result from a decrease in suitable cover through space and time. The complexity of ecological systems makes area-specific and species-specific estimates of these characteristics highly desirable in meeting the challenges of wildlife management.

Further, "home range size likewise varies by sex and age of the individual, habitat, and season" (Demarais et al. 2000:610), so specific information about space use may be the most helpful for guiding management objectives and decisions.

The increasing size of white-tailed deer (*Odocoileus virginianus*) and human populations coupled with increasing land-use changes (e.g., urbanization) further add to the complexity of deer management across much of the United States (Demarais et al. 2000). Because these attributes can vary greatly across a landscape, management agencies often develop species-specific management units within a state and apply their management objectives accordingly. Although management-unit boundaries are often based on non-ecological components of the landscape, such as roads or county boundaries, these features are often more transparent to consumptive users of wildlife and other stakeholder groups. Ecological boundaries could, for example, be based on areas containing source and sink populations, areas containing low-quality habitat, or incorporating ecological barriers that might restrict animal movements. Managers often assume or have evidence that the species of interest has population characteristics that differ across the landscape, and consequently, the management of this species often differs by management unit. Management-unit boundaries, even if based on non-ecological components, are often adapted by state agencies over time to more accurately reflect wildlife population dynamics and land-use patterns.

Management of high deer populations through regulated hunting is probably the most cost-effective strategy (Demarais et al. 2000). Harvest objectives are normally implemented at the management-unit level and may be age- and sex-specific for deer. For example, harvest objectives for antlerless deer (i.e., males <1 yr old and females) are often adapted to achieve the agency's population goals, such as when the deer population is determined to be higher than desired. Knowledge of population characteristics of deer, especially female deer, under these circumstances is important as female deer are often the sex class of primary interest for managers desiring relatively large reductions in population densities through hunter-harvest (Carpenter 2000).

My objectives were to describe age-specific survival, cause-specific mortality, and space use of female white-tailed deer in south central Michigan, and to compare my findings with past research on deer in Michigan. I used female white-tailed deer for analyses, as south central Michigan currently has a relatively high deer density (~27/km^2 during fall 2005; Michigan Department of Natural Resources [MDNR] 2005), and the southern Michigan deer population is generally above the desired population goals of the MDNR (Clute 2006).

STUDY AREA

My study was conducted in eastern Jackson (Grass Lake, Henrietta, and Waterloo townships), western Washtenaw (Dexter, Lima, Lyndon, and Sylvan townships), and southwestern Livingston (Unadilla township) counties in south central Lower Michigan (Fig. 1.1). The study area (82,636 ha) included publicly owned lands, including the MDNR Waterloo (8,410 ha; 10.2% of study area) and Pinckney (4,276 ha; 5.2%) recreation areas, and privately owned lands. South central Michigan has been characterized by a relatively high deer density, increasing land-use activities (e.g., urbanization), and little scientific study of deer under these conditions. Although the study area was primarily rural (98% of total land area), the human population increased 16% and housing units increased 22% between 1990 and 2000 (U.S. Census Bureau

2003). Much of the landscape throughout southern Michigan (and in other areas throughout the Midwest) is expected to experience increasing land-use activities similar to the study area (Madill and Rustem 2001).

The physiographic regions of this area are Hillsdale-Lapeer Hilly Upland, South Central Rolling Plain, and Southeastern Rolling Plain (Sommers 1977:24) with alfisols as the major soil order (Sommers 1977:36). Surface formations in the study area are the result of glaciation and include all 4 types present within Michigan (moraine, till plain, outwash plain, and lacustrine plain; Sommers 1977:32). Elevation of the study area ranged approximately 180–300 m and consisted of relatively limited relief (Sommers 1977:26, 33). The study area received about 81 cm of precipitation annually during 1971–2000 (based on conditions in Chelsea, Michigan; Midwestern Regional Climate Center, Champaign, Illinois, USA), and had a 150-day growing season (i.e., the average annual accumulation of daily mean temperatures >5.6 °C), generally occurring from 10 May to 7 October (Sommers 1977:46, 49). During 1971–2000, average annual snowfall was 99.3 cm and mean monthly temperatures ranged from –5.4 °C (Jan) to 21.8 °C (Jul) in Jackson County (Midwestern Regional Climate Center, Champaign, Illinois, USA). Total annual snowfall during my study was highly variable (2004 = 90.9 cm, 2005 = 149.9 cm, 2006 = 40.0 cm; conditions in Chelsea, Michigan; Midwestern Regional Climate Center, Champaign, Illinois, USA).

Before European settlement, southern Michigan forests consisted of oak (*Quercus* spp.) and hickory (*Carya* spp.) in well-drained soils and beech (*Fagus grandifolia*), elm (*Ulmus* spp.), maple (*Acer* spp.), and basswood (*Tilia americana*) in poorly drained soils (Sommers 1977:17). Much of the study area is well suited for agriculture (Sommers

1977:38). Most crop agriculture in Jackson and Washtenaw counties (total area = 366,483 ha) is in corn (37,840 ha) and soybean (34,200 ha) production, followed by hay (17,200 ha), winter wheat (7,970 ha), and oats (930 ha; Michigan Department of Agriculture 2002).

I generalized land-use, land-cover data (Michigan Center for Geographic Information 2001) using ArcView GIS v3.2 software (Environmental System Research Institute, Redlands, California, USA) and Spatial Analyst extension to define 13 cover types within the study area (Fig. 1.1): agriculture (non-vegetated farmland, row crops, forage crops; 52.3% of study area); conifer (pines [*Pinus* spp.], other upland conifers; 1.5%); herbaceous openland (herbaceous vegetation with <25% woody cover; 2.9%); lowland deciduous forest (>60% composed of deciduous tree cover; 8.0%); lowland shrub (with >60% non-water cover; 9.9%); mixed wetland (floating aquatic vegetation, emergent wetland, mixed non-forest wetland; 3.1%); northern hardwood (>60% canopy cover of maple, beech, ash [*Fraxinus* spp.], cherry [*Prunus* spp.], birch [*Betula* spp.]; 2.3%); oak association (>60% canopy cover of oak; 1.6%); upland deciduous forest (>60% canopy cover of upland deciduous trees; 11.6%); upland shrub (>25% woody cover; <0.1%); urban (low and high intensity, roads, parks, golf courses; 2.8%); water (surface, flowing; 3.9%); and other (aspen [*Populus* spp.] association, orchards, bare ground; 0.1%). Patch size of cover types ranged from <1 ha to >11,000 ha (e.g., an agricultural matrix) and had a mean size of 29.2 ha. Consequently, generalization of spatial data may have excluded certain fine-scale landscape characteristics (e.g., hedgerows, roads) in some instances.

METHODS

Capturing Deer

Winter.—Technicians and I trapped deer during winter (Dec–Mar) 2004–2006, using single-door collapsible live traps (Clover 1954). Traps were placed near areas of deer activity, baited with kernel corn, and checked twice/day to minimize stress and injury to deer. We restrained captured deer using the collapsed trap and the body weight of 1 person (Sparrowe and Springer 1970). All trapped deer were blindfolded to reduce stress and fitted with metal ear tags bearing a unique identification number (Style 681; National Band and Tag, Newport, Kentucky, USA). Individuals were aged as fawn (<1 year old), yearling (≥1–<2 years old), or adult (≥2 years old) through general morphometric differences (e.g., shape and size of head, body size) and dental characteristics (Severinghaus 1949); ages of necropsied individuals later confirmed accuracy of field observations for deer captured during winter.

Only female deer were fitted with mortality-sensing collar-style radio-transmitters, either with VHF (Model 500; Telonics, Inc., Mesa, Arizona, USA) or VHF-GPS (Model G2000; Advanced Telemetry Systems, Isanti, Minnesota, USA) capabilities. I did not radiomark male deer because I expected low capture success for adult males when using Clover traps (T. Hiller, unpublished data). Additionally, winter-captured male deer were not radiomarked because of potential problems associated with their physiological changes (i.e., neck-swelling) during the breeding season and fitting a radio-transmitter to deer for these changes. Radio-transmitters had a unique frequency within the 150-MHz range, a mass of 270 g (VHF) or 1,100 g (VHF-GPS), and an expected minimum battery life of 36 months (VHF) or 12 months (VHF-GPS).

Spring.—The capture season for neonatal fawns was from mid-May to mid-June 2004–2006. I expected capture success to peak around 1 June and instances of fawns flushing to increase greatly after mid-June (Pusateri Burroughs et al. 2006), thus reducing my ability for successful capture; fawns >2 weeks old generally start flushing when approached by humans (Carroll and Brown 1977). Technicians and I captured neonates either by hand or in a fish-landing net (0.5-m-diameter net, 2-m-long extendable handle). A group of 2–6 people systematically searched potential fawning areas (e.g., areas transitioning from forest to wetland or grassy field) for neonates (Lund 1975, Ballard et al. 1999). Isolated adult females occasionally provided behavioral signs of a nearby fawn (e.g., a doe looking toward an area several times/min; Downing and McGinnes 1969).

I weighed, sexed, ear-tagged (Style 681; National Band and Tag, Newport, Kentucky, USA) and radiomarked each captured neonate. Captured neonates also were aged using hoof-growth measurements (Haugen and Speake 1958). The mortality-sensing radio-transmitters (Model M4210; Advanced Telemetry Systems, Isanti, Minnesota, USA) had an expandable collar to allow for growth and were designed to drop off after 9–12 months for retrieval (see Diefenbach et al. 2003). Transmitters had a unique frequency within the 151-MHz range, a mass of 60 g, and an expected minimum battery life of 12 months. The precise-event transmitter option provided a time-of-mortality estimate within 30 min for a maximum of ~5 days post-mortality (i.e., 5 days of no transmitter movement).

Neonates were classified as fawns at the time of capture, but were reclassified when they reached 1 June of the first year (yearling) or second year (adult) following capture. Similarly, winter-captured deer were reclassified to the next age class each time they reached 1 June following capture. Michigan State University's All-University Committee on Animal Use and Care approved all capturing and handling procedures for my study (Application No. 01/04-006-00).

Survival and Cause-specific Mortality

All deer were monitored 2–5 times/week to estimate survival and assess cause-specific mortality, but spring-captured fawns were monitored daily for the first 30 days following capture to potentially increase the accuracy of assessments. I used the Mayfield method (Mayfield 1961, 1975), modified by Bunck and Pollock (1993) for censored individuals, to estimate survival of deer. Daily survival was estimated for 3 time periods for fawns (0–6 months old [Chapter 2], 6–12 months old, annual), and annually for yearlings and for adults. For analyses, I excluded any individual that died within a 7-day acclimation period following capture. Individuals were censored if I believed they were alive at the time of transmitter recovery (e.g., the break-away collar dropped), at the conclusion of field data collection, or when they moved into the next age class.

My assessment of cause-specific mortality of recovered carcasses was based on my field observations and the necropsies performed by a wildlife pathologist (MDNR Wildlife Disease Laboratory, East Lansing, Michigan, USA). I classified mortalities of individuals into 5 categories: canid (coyote [*Canis latrans*], red fox [*Vulpes vulpes*], gray fox [*Urocyon cinereoargenteus*], or domestic dog [*C. lupus familiaris*]) predation, trauma or malnutrition (e.g., abandonment), vehicle collision, hunter-harvest, and unknown. If I did not have enough post-mortality evidence to ascribe cause with reasonable certainty (e.g., total consumption of the carcass), then I considered the cause of mortality to be unknown.

Space Use

Technicians and I estimated locations of deer 2–5 times/week using triangulation from telemetry signals (White and Garrott 1990:79–112) or from visual observations of known individuals. To increase the accuracy of space-use assessment, we located deer in a systematic manner during varying time schedules on a diel basis (Beyer and Haufler 1992), with ≥ 1 nocturnal location/deer/week, except during capture periods. Bearings were estimated using a 3-element folding Yagi antenna (Advanced Telemetry Systems, Incorporated, Isanti, Minnesota, USA), portable radio receiver (Model R-1000, Communications Specialists, Incorporated, Orange, California, USA), and mirror-sighting compass. A global positioning system (GPS) handheld unit (Model GPS IV; GARMIN International, Incorporated, Olathe, Kansas, USA) was used to approximate the locations from which signals were received.

I used the program LOCATE III (Pacer, Truro, Nova Scotia, Canada) to estimate locations of deer using triangulated data based on the maximum likelihood estimator (Lenth 1981*a*,*b*), as recommended by White and Garrott (1990) and Nams and Boutin (1991). During analysis, I also used LOCATE III to estimate bearing standard deviations and error ellipses for location estimates. I based telemetry-error assessments on the relationship between mean error-ellipse size and mean landscape-patch size to determine if I had appropriate sample sizes (see Nams 1989).

Space use is often estimated using 1 of the many home-range estimators (e.g., minimum convex polygon, kernel methods, harmonic mean), but each may provide different results using the same data. I used the fixed-kernel method, which seems to be the best estimator currently in use based on the criteria outlined by Kernohan et al. (2001), and least-squares cross-validation to determine the smoothing parameter (Worton 1995, Seaman et al. 1999). My description of space use included only individuals with ≥ 30 locations (Seaman et al. 1999).

Space-use data were pooled by age class and season based on agricultural crop production (i.e., the growing season on study area [10 May–7 Oct; 150 d], and the non-growing season [8 Oct–9 May; 215 d]). I assumed that all location estimates that were classified in the cover type water were inaccurate and I relocated each to the nearest alternative cover type. Only location data from VHF signals were used to avoid potential differences associated with location precision between VHF- and GPS-derived location estimates (i.e., I used only VHF-derived data from VHF-GPS transmitters).

I used Animal Movement extension in ArcView GIS v3.2 software (Environmental System Research Institute, Redlands, California, USA) to estimate space use. For all statistical analyses, I used SYSTAT v11 (Systat Software, Inc., San Jose, California, USA) and ProStat v4.02 (Poly Software International, Inc., Pearl River, New York, USA). Unless noted otherwise, I used 95% confidence limits (CLs; LCL = lower, UCL = upper) during my statistical analyses. The use of confidence limits is advantageous in that an estimate of effect size and a measure of uncertainty are provided (Johnson 1999).

RESULTS

Capture and Estimation of Locations

I captured and radiomarked 42 female deer during winter 2004–2006 (Table 1.1) and 34 neonates during spring 2004–2006 (Table 1.2). Two neonates and 2 winter-captured deer died <7 days post-capture and were excluded from analyses. I pooled spring-captured animals by sex (56% male) and assumed behavioral differences were minimal or nonexistent between male and female fawns (see Ozoga and Verme 1986) during the agricultural growing season, after which males were excluded from analyses. I pooled data by age class and season but could not consider year effects due to small sample sizes.

Survival and Cause-specific Mortality

Survival was lower for fawns 0–6 months old (0.67 for 6-month survival; 95% CL = 0.51–0.84; n = 32; Chapter 2) than for fawns 6–12 months old (0.90; 95% CL = 0.78–1.00; n = 23); annual fawn survival was estimated to be 0.51 (95% CL = 0.37–0.66; n = 48). Annual survival estimates for yearlings and adults were 0.94 (95% CL = 0.85–1.00; n = 28) and 0.56 (95% CL = 0.38–0.75; n = 28), respectively.

The primary annual source of mortality for fawns was vehicle collisions (64% of mortalities), and fawns were the only age class depredated by canids (Table 1.3). Of the 12 yearlings radiomarked, only 1 died, with the cause assessed as malnutrition related to trauma. Eleven of 13 (85%) adults that died were harvested by hunters. Mortalities related to capture or radio-collar trauma seemed least prevalent with adults (Table 1.3).

Space Use

Telemetry-error assessment.—I pooled all location estimates (8,714) from deer of all ages (n = 66) from my study to estimate overall telemetry error. The mean error-ellipse size was 10.2 ha. I considered telemetry error acceptable, and thus, location estimates of acceptable precision, given the landscape characteristics of the study area (e.g., $\bar{x}$ = 29.2 ha/patch) and the number of location estimates ($\bar{x}$ = 132/deer). This conclusion was based on the relationship between telemetry error and patch size to determine appropriate sample sizes as described by Nams (1989). Further, given the patchiness of the study area, I assumed that characteristics of each cover type (e.g., differences in foliage densities) did not influence our telemetry accuracy, resulting in acceptance of location estimates near cover-type boundaries as accurate even if error ellipses covered ≥ 1 cover type (White and Garrott 1990:200).

Within age class.—Seasonal home-range differences existed for fawns, yearlings, and adults (Tables 1.4, 1.5, and 1.6, respectively). Within the fawn and adult age classes, the growing season mean home-range size was approximately half that of the non-growing season mean home-range size (Tables 1.4 and 1.6). Yearlings had similar mean home-range sizes for the growing (201.8 ha) and non-growing (156.88 ha) seasons (Table 1.5), but variation was large (SE = 91.1 and 28.2, respectively). Ninety-five percent CLs of seasonal home ranges overlapped within each age class, but only slightly for adults (Table 1.6). The mean amount (ha) of upland deciduous forest cover within kernel home ranges quadrupled for fawns from the growing to the non-growing season (Table 1.4). Yearlings selected 2 cover types in different proportions (Table 1.5): agricultural areas were selected at twice the proportion during the growing season (0.26) than during the non-growing season (0.12), while upland deciduous forests were selected in a higher proportion during the non-growing season (0.33 versus 0.19). Other cover types were selected in similar proportions within each age class.

Among age classes.—Fawn home ranges during the growing season (Table 1.4) were smaller than both yearling and adult non-growing season estimates (Tables 1.5 and 1.6). The yearling non-growing season estimate was only slightly larger than the adult growing-season estimate based on 95% CLs, indicating a minor transition in home-range size through time. Many differences in the amounts (ha) of each cover type in home ranges existed across age classes. Based on CLs, fawn home ranges during either season had compositional differences in herbaceous openlands, lowland shrubs, northern hardwoods, and upland deciduous forests with the composition of ≥ 1 seasonal home range of other age classes. Two other age-specific differences in home-range cover composition existed: yearlings during the non-growing season used more northern hardwoods (8.4 ha) and lowland deciduous forests (25.9 ha) than adults (2.9 and 4.7 ha, respectively) during the growing season.

Home-range trends.—Mean home-range sizes showed an oscillatory pattern based on age and season, with home-range size greatest for yearlings during the growing season (Fig. 1.2). Regardless of age, deer movements generally seemed to increase during fall and peaked soon after hunters expended the most effort for harvest (i.e., following regular firearms season: ~30 Nov) in Lower Michigan. I assumed home-range size by season was consistent for adults regardless of actual age, and extrapolated the pattern to be consistent for all deer >2 years old.

DISCUSSION

Without research, managers may not have suitable information describing how population characteristics vary substantially across a landscape. If demographic information is not available on an area-specific and age-specific basis, then estimates based on the available literature must be used for management. For example, the sex-age-kill model (SAK; Creed et al. 1984, Skalski et al. 2005) is often used to estimate deer abundance within a management unit by using variables associated with demographics (e.g., annual survival, harvest mortality), various age and sex ratios, harvest data, and other population characteristics. Of course, the estimates of abundance from SAK are only as accurate as the input estimates. If population characteristics of deer differ among management units (or otherwise across landscapes) and through time, then with accurate data this model should theoretically calculate these differences in abundance and management objectives (e.g., harvest quotas) may then be adapted for the following year.

Demographics may vary according to many variables (e.g., habitat quality and seasonal weather patterns [Demarais et al. 2000], population trends [McCullough 2001]), so management objectives and practices should be adapted accordingly. Although extrapolation of data is often necessary, as species-specific research cannot (and probably should not) be conducted at a fine spatial scale across an entire state due to financial constraints, certainly comparisons among within-state research projects should provide insight into patterns of wildlife population dynamics, especially in relation to land-use activities. Additionally, if the spatial scale of study is too fine, the study design may not reflect the natural history of the species under study (e.g., as the defined spatial extent of availability is reduced, resource selection may become more difficult to detect [McClean et al. 1998]).

Michigan Deer Research

The white-tailed deer is the most popular big-game species in North America (Smith and Coggin 1984, U.S. Fish and Wildlife Service 2001). Its status in Michigan is no different, with about 743,000 hunters harvesting nearly 500,000 deer in 2003 (Frawley 2004). Not surprisingly, Michigan has a strong tradition of deer research that has been conducted throughout the state, especially during the past decade. Demographics and space use of free-ranging deer are often most easily estimated using radiomarked individuals and numerous studies have been conducted in Michigan using telemetry techniques. Research in the Upper Peninsula has included seasonal migrations and mortality of deer (Van Deelen et al. 1997, Van Deelen et al. 1998) as well as their habitat use and browsing effects (Mackey 1996). In the Northern Lower Peninsula, Sitar (1996) and Sitar et al. (1998) examined the seasonal movements, habitat use, and population characteristics of deer, while Garner (2001) and Muzo (2003) examined the movements and behavior of a bovine tuberculosis-infected deer population.

The most recently completed field study was a description of the population characteristics and landscape-use patterns of deer on private lands in southwestern Lower Michigan (Pusateri 2003, Pusateri Burroughs et al. 2006). Pusateri (2003) and Pusateri Burroughs et al. (2006) research on nonmigratory deer in southwestern Lower Michigan are the most comparable to my results based on deer behavior and landscape similarity; e.g., deer in the Upper and northern Lower Peninsulas frequently migrate between summer and winter home ranges for sufficient winter thermal cover (Verme 1973, Van

Deelen et al. 1998), while thermal cover may not be necessary for deer in southern Lower Michigan (Torgersen and Porath 1984). Migratory behavior will affect space-use assessments and often estimates of demographics; differences in cover types, agricultural growing season, and landscape characteristics (e.g., patch size and shape) may also affect population characteristics.

Age-specific Characteristics

Fawns.—Until now, Pusateri Burroughs et al. (2006) has been the only study that described survival, cause-specific mortality, or space use of young free-ranging white-tailed deer fawns in Michigan. With data pooled over 2 years, they estimated annual fawn survival on privately owned lands at 0.75 (95% CL = 0.59–0.91; Kaplan-Meier method) in southwestern Lower Michigan, much higher than my estimate of 0.51 (95% CL = 0.37–0.66). Cause-specific mortality sources for fawns <1 year were also different between studies, with higher mortality due to hunting (29%) and lower mortality due to vehicle collisions (29%) compared to my study (18% and 64%, respectively). Potential reasons for these differences may include higher densities of humans ($\bar{x}$ = 1.39/ha versus $\bar{x}$ = 1.00/ha; U.S. Census Bureau 2006) and deer (~27/km^2, MDNR 2005; ~19/ km^2, Pusateri 2003) on my study area, as well as differences in land-ownership and land-use patterns (e.g., hunting opportunities might increase with an increase in amount of public land on an area). Deer habitat quality and the amount of traffic on roadways, both positively related to deer-vehicle collisions in southern Lower Michigan (Sudharsan 2005), and likely elsewhere, also probably contributed to differences in cause-specific mortality between study areas. Other mortality sources contributed little to overall mortality for deer <1 year old during both studies.

Although Pusateri Burroughs et al. (2006) estimated the mean home-range size of 27-week-old fawns (62.7 ha; ~May–Dec), their estimate was similar to my growing season (~May–Oct) estimate of 60.2 ha. Cover composition within kernel home ranges varied between studies, as my estimates contained more conifers (22% versus 10%) and less agriculture (32% versus 46%) and deciduous forests (23% versus 40%). Although not directly comparable because of differing time intervals, their mean annual home-range size estimate (75.4 ha) was only 65% of my mean non-growing season home-range estimate (116.3 ha) for fawns. Differences in cover availability likely contributed to some cover selection differences between study areas.

Yearlings.—Survival estimates of yearling deer within the Lower Peninsula of Michigan seem limited. Pooled by sex, annual survival of yearlings for a 2-year study (Sitar 1996; northern Lower Michigan) ranged from 0.29 (95% CL = 0.10–0.48) to 0.36 (95% CL = 0.18–0.54), which were both much lower than my pooled annual estimate (95% CL = 0.85–1.00). Sitar (1996) stated that yearling survival may have been somewhat overestimated due to mild winter conditions during her study, which suggested that long-term differences between our estimates may be even more pronounced. Long-term (1971–2000) winter conditions (e.g., mean monthly temperatures, mean annual snowfall) on her study area (Jan = –7.9 °C, annual snowfall = 142.2 cm; Alpena County; Midwestern Regional Climate Center, Champaign, Illinois, USA) were generally more severe than on my study area (Jan = –5.4 °C, annual snowfall = 99.3 cm; Jackson County; Midwestern Regional Climate Center, Champaign, Illinois, USA). Age- and sex-specific survival estimates of migratory deer in Michigan's Upper Peninsula showed that yearling females had a high annual survival rate (0.89) in comparison to other age-sex classes

(Van Deelen 1995); he also found that non-hunting mortality did not differ between sexes, but annual hunting mortality was much higher for males. To my knowledge, cause-specific mortality and space use have not been assessed specifically for yearling white-tailed deer in southern Lower Michigan.

Adults.—Deer >6 months old (i.e., yearlings and adults) in southwestern Lower Michigan had annual survival estimates (Kaplan-Meier method) that ranged from 0.40 (95% CL ≈ 0.20–0.60) to 0.77 (95% CL ≈ 0.61–0.93) (data pooled by sex; Pusateri 2003). Using the Mayfield method, Sitar (1996) estimated annual survival of adult deer in the northern Lower Peninsula of Michigan to be 0.53 (95% CL = 0.37–0.69) and 0.71 (95% CL = 0.50–0.92), depending on year. My survival estimate for adult females (0.56; 95% CL = 0.38–0.75) was generally consistent with these estimates.

Cause-specific mortality for female deer >6 months old (n = 48; 18 died) included hunter-harvest (61% of mortalities), vehicle collisions (28%), and trauma-related injuries (11%) in southwestern Lower Michigan (Pusateri 2003). In northern Lower Michigan, the 4 most prominent known mortality sources for male and female deer included hunter-harvest (37% of mortalities), natural causes (e.g., predation, drowning; 24%), illegal harvest (12%), and vehicle collisions (10%; Sitar 1996). The only significant cause of mortality on my study area for adult female deer was hunter-harvest (85% of mortalities). Based on radiomarked individuals, adults were also the age class of females most harvested by hunters, as only 2 fawns and no yearlings were harvested during my 3-year study. Break-away collars on spring-captured fawns dropped off at an average of 354.7 days (SE = 54.6; Chapter 2), well after the first hunting season that these fawns experienced.

I found that home-range sizes of adult females during the non-growing season (140.4 ha) were approximately twice the size of home ranges during the growing season (77.5 ha). Adult female deer often restrict movements near and following parturition (Marchinton and Hirth 1984), which may explain this difference in space use. Increases in time spent foraging due to increased energetic demands during the breeding season and potentially limited food resources during winter may also have caused increased movements. Interestingly, the mean proportion of each cover type within home ranges differed little by season for adults, suggesting that although movements increased, cover selection (i.e., based on selection indices) remained relatively constant.

My non-growing-season adult home-range estimate (140.4 ha) was similar in size to the annual estimates of deer >6 months old (157.7 ha; non-dispersers; $n = 53$; 91% females) in southwestern Lower Michigan (Pusateri 2003). However, cover composition within home ranges differed somewhat. Home ranges in southwestern Lower Michigan consisted of a higher percentage of agricultural areas (39% versus 20%) and deciduous forests (47% versus 37% [upland and lowland combined]), but less conifer cover (<4% versus 8%) compared to my results. Lowland-shrub cover composed a large percentage of my adult home ranges (~23% during both seasons), but this cover type was not defined by Pusateri (2003). Comparisons of cover use to other studies in Michigan would be less meaningful, as they were conducted in northern latitudes where deer often exhibit migratory behavior and cover types become increasingly different.

Age-specific Trends

Although the confidence limits of age-specific home-range sizes often overlapped somewhat, there was useful information in the age-specific trends. Trends in mean home-range size of individuals over time on my study area were consistent with broad descriptions of deer movements. "Young fawns have small home ranges, but as they get older their ranges begin to approximate that of their dams. Yearlings and young adults may move over larger areas than do older adults, at least in localities where extreme seasonal range shifts are common" (Marchinton and Hirth 1984:131), insinuating a trend similar to deer on my study area. Demarais et al. (2000) stated that home-range size varied by age of individuals of a species and season, which I found to be true; the comparison of my results to other Michigan deer studies also supported their assertion that habitat (conditions) and sex of individuals also affects home-range sizes.

Yearling females had relatively large home-range sizes (Fig. 1.2), as expected (Marchinton and Hirth 1984). Although it may be counterintuitive that that these movement patterns would be coupled with the highest survival (0.94) among age classes, sources of age-specific mortality may provide an explanation. The primary sources of mortality for fawns and adults were vehicle collisions and hunter-harvest, respectively. Deer may be more susceptible to vehicle collisions until some type of avoidance behavior has been established, which may occur during the juvenile stage. Further, adults may be the age class of antlerless deer selected by or more available to hunters, as suggested by my data (Table 1.3).

I expected differences in survival and cause-specific mortality among age classes, but the magnitude of these differences was unknown, as were the relative differences when making comparisons with other studies of deer ecology in Michigan. The information that I have provided should help inform deer managers in Michigan and other areas of the Midwest experiencing increasing urbanization, as the population characteristics of white-tailed deer in an increasingly urbanizing landscape were largely unknown.

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Table 1.1. Comparison of 3 winter capture seasons of white-tailed deer (*Odocoileus virginianus*) using Clover traps during 2004–2006, south central Michigan, USA.

Season	Date	Trap-days	Females radiomarked	Total captures	Recapture events	Trapping success[a]
1	28 Jan–26 Mar 2004	520	12	19	11	0.037
2	17–21 Dec 2004, 4 Jan–24 Mar 2005	647	22	34	19	0.052
3	9 Jan–22 Mar 2006	659	8	16	5	0.024
Total		1826	42	69	35	0.038

[a] $\text{Trapping success} = \dfrac{\text{Total number of captured deer}}{\text{Total number of trap-days}}$

Table 1.2. Comparison of 3 spring capture seasons of neonatal white-tailed deer (*Odocoileus virginianus*) during 2004–2006, south central Michigan, USA.

		Neonates			Effort[a]	
Season	Date	Observed	Radiomarked	% male	Total	Per neonate[b]
1	11 May–23 June 2004	18	9	56	358.5	39.2
2	10 May–17 June 2005	18	10	60	308.1	30.8
3	9 May–5 June 2006	19	15	53	184.9	12.3
Total		55	34		851.5	$\bar{x} = 25.0$

[a] Observer-hours

[b] Radiomarked neonates only

Table 1.3. Fate assessment of radiomarked female white-tailed deer (*Odocoileus virginianus*) based on age class (fawn = <1 yr, yearling = ≥ 1 yr–<2 yr, adult = ≥2 yr), south central Michigan, 2004–2006.

	Age class[a]		
Fate	Fawn (*n* = 32)	Yearling (*n* = 12)	Adult (*n* = 28)
Mortality			
Hunter-harvest	2	0	11
Vehicle collision	7	0	1
Trauma or malnutrition	0	1	1
Canid predation[b]	2	0	0
Total	11	1	13
Censored			
Collar slipped/removed[c]	9	6	6
Lost signal	3	1	3
Alive at end of study	6	2	5
Capture myopathy, collar trauma (mortality)	3	2	1
Total	21	11	15

[a] At time of fate assessment.

[b] Included coyote (*Canis latrans*), red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), and domestic dog (*C. lupus familiaris*).

[c] Removed collars included break-away radio-transmitters designed to drop off after 9–12 months and remotely removed GPS collars after 1 yr of use.

Table 1.4. Space use (95% fixed-kernel home ranges) and cover composition of female fawn (<1 yr old) white-tailed deer (*Odocoileus virginianus*) during the agricultural growing (10 May–7 Oct; $n = 28$) and non-growing (8 Oct–9 May; $n = 21$) seasons, southern Michigan, 2004–2006.

Season	Kernel home range size (ha)		
Cover type	$\bar{x}$	95% LCL	95% UCL
Growing	60.24	31.23	89.26
Agriculture	19.20	8.16	30.24
Conifer	13.15	5.67	20.64
Herbaceous openland	0.19	0.00	0.44
Lowland deciduous forest	9.33	3.14	15.53
Lowland shrub	4.61	1.93	7.30
Mixed wetland	4.42	0.00	9.47
Northern hardwood	2.29	1.25	3.32
Oak association	0.69	0.00	1.57
Upland deciduous forest	4.50	2.51	6.48
Upland shrub	0.00		
Urban	0.18	0.00	0.43
Water	1.49	0.00	3.25
Other	0.00		
Non-growing	116.26	73.33	159.19
Agriculture	21.55	12.70	30.41

Table 1.4. (cont'd)

Season	Kernel home range size (ha)		
Cover type	$\bar{x}$	95% LCL	95% UCL
Non-growing			
Conifer	15.89	6.47	25.31
Herbaceous openland	4.99	0.79	9.18
Lowland deciduous forest	16.49	7.33	25.65
Lowland shrub	18.47	3.85	33.09
Mixed wetland	7.75	0.00	19.27
Northern hardwood	4.24	2.77	5.72
Oak association	2.98	1.29	4.67
Upland deciduous forest	22.55	13.44	31.67
Upland shrub	0.00		
Urban	0.11	0.00	0.34
Water	0.83	0.00	1.87
Other	0.04	0.00	0.10

Table 1.5. Space use (95% fixed-kernel home ranges) and cover composition of female yearling (≥ 1–<2 yr old) white-tailed deer (*Odocoileus virginianus*) during the agricultural growing (10 May–7 Oct; *n* = 12) and non-growing (8 Oct–9 May; *n* = 15), southern Michigan, 2004–2006.

Season	Kernel home range size (ha)		
Cover type	$\bar{x}$	95% LCL	95% UCL
Growing	201.82	1.25	402.38
Agriculture	51.74	0.00	113.62
Conifer	19.22	0.00	40.56
Herbaceous openland	2.86	0.51	5.20
Lowland deciduous forest	23.78	0.00	52.86
Lowland shrub	36.27	3.31	69.22
Mixed wetland	10.24	0.00	20.51
Northern hardwood	11.19	0.00	26.04
Oak association	3.70	0.00	10.25
Upland deciduous forest	37.62	1.10	74.14
Urban	0.00		
Water	5.10	3.95	13.79
Other	0.10	0.00	0.32
Non-growing	156.88	96.35	217.41
Agriculture	18.34	5.10	31.59
Conifer	13.59	1.46	25.72

Table 1.5. (cont'd)

Season Cover type	Kernel home range size (ha) $\bar{x}$	95% LCL	95% UCL
Non-growing			
Herbaceous openland	4.26	0.72	7.79
Lowland deciduous forest	25.89	8.99	42.80
Lowland shrub	23.33	9.83	36.82
Mixed wetland	3.48	0.00	7.05
Northern hardwood	8.42	5.01	11.82
Oak association	4.02	0.92	7.11
Upland deciduous forest	52.19	29.07	75.30
Upland shrub	0.00		
Urban	0.09	0.00	0.27
Water	3.21	0.00	6.56
Other	0.08	0.00	0.25

Table 1.6. Space use (95% fixed-kernel home ranges) and cover composition of female adult (>2 yr old) white-tailed deer (*Odocoileus virginianus*) during the agricultural growing (10 May–7 Oct; *n* = 23) and non-growing (8 Oct–9 May; *n* = 25), southern Michigan, 2004–2006.

Season	Kernel home range size (ha)		
Cover type	$\bar{x}$	95% LCL	95% UCL
Growing	77.51	57.46	97.56
Agriculture	11.23	4.57	17.90
Conifer	8.18	2.28	14.08
Herbaceous openland	0.28	0.00	0.63
Lowland deciduous forest	4.69	1.52	7.85
Lowland shrub	17.50	9.47	25.53
Mixed wetland	2.74	0.00	6.90
Northern hardwood	2.92	1.45	4.39
Oak association	1.42	0.32	2.52
Upland deciduous forest	27.12	15.26	38.99
Upland shrub	0.00		
Urban	0.12	0.00	0.29
Water	1.32	0.02	2.61
Other	0.00		
Non-growing	140.39	91.58	189.20
Agriculture	27.77	13.76	41.77

Table 1.6. (cont'd)

Season	Kernel home range size (ha)		
Cover type	$\bar{x}$	95% LCL	95% UCL
Non-growing			
Conifer	10.83	4.35	17.31
Herbaceous openland	1.26	0.00	2.61
Lowland deciduous forest	8.47	4.14	12.80
Lowland shrub	33.50	17.87	49.14
Mixed wetland	6.05	0.10	11.99
Northern hardwood	3.86	1.98	5.74
Oak association	2.25	1.23	3.27
Upland deciduous forest	43.89	25.47	62.31
Upland shrub	0.00		
Urban	0.14	0.00	0.34
Water	2.39	0.61	4.17
Other	0.00		

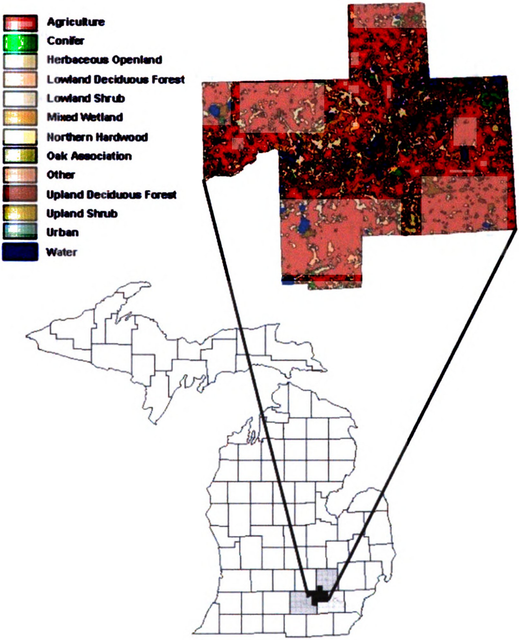

Figure 1.1. Study area location and distribution of cover types, south central Michigan, USA, 2004–2006. Study-area boundary was defined to include any township containing ≥ 1 radiomarked white-tailed deer (*Odocoileus virginianus*) location estimate.

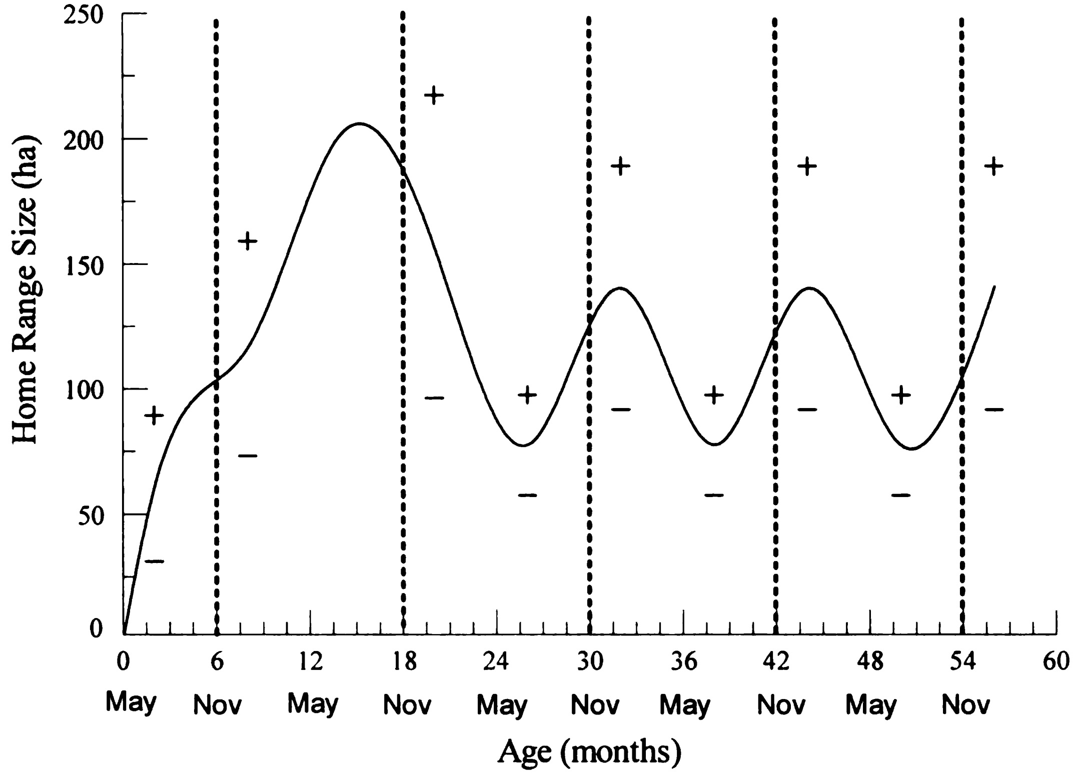

Figure 1.2. Pattern of home-range size estimates of white-tailed deer based on mean size and 95% CLs (− = lower, + = upper) of 3 age classes (fawn = 0–12 months old, yearling = 12–24 months old, adult = >24 months old) pooled through time during the growing (~May–Oct) and non-growing (~Oct–May) agricultural seasons, south central Michigan, USA, 2004–2006. Vertical dashed lines approximate the regular firearms deer season (15–30 Nov).

CHAPTER 2

Survival and Space Use of Fawn White-tailed Deer in Southern Michigan

Survival and Space Use of Fawn White-tailed Deer in Southern Michigan

INTRODUCTION

Most members of the deer family (Cervidae) and other ungulates have similar patterns of behavior near and following parturition. Neonatal ungulate behavior includes either following the dam or hiding to reduce their conspicuousness to predators; most cervids exhibit the latter behavior (Lent 1974). Moose (*Alces alces*), elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) adult females often isolate themselves from intraspecifics, the young rely on cover and cryptic coloration as their primary defenses against predation, and the dam visits offspring periodically for feeding and grooming. After a certain degree of development, young cervids progressively increase activity and movements, primarily while accompanying the dam; adult male deer generally exhibit behaviors and space use independent of the young (see Franzmann 1981, Marchinton and Hirth 1984, Smith 1991, Demarais and Krausman 2000).

Fawn white-tailed deer (hereafter, deer) and their dams express consistent behaviors through the first 2 months postpartum. Fawns ≤2 months old are sedentary and associate infrequently with their dams (Schwede et al. 1994); Jackson et al. (1972) found that fawns in this age class had activity patterns dissimilar to adult females, and that fawns often were active ≤20% of the time. Twins are maintained at separate localities during the first 3–6 weeks (Ozoga et al. 1982, Marchinton and Hirth 1984) and adult females often establish territories surrounding their fawns for approximately the first month (Ozoga et al. 1982, Marchinton and Hirth 1984). Fawns are functional ruminants around 2 months of age (Short 1964), suggesting decreasing dependence on the dam. Fawn survival may increase significantly after the first 8 weeks (Carroll and Brown 1977), as they may be better able to elude predators (Nelson and Woolf 1987). Low survival of fawns may decrease recruitment enough to affect deer population dynamics (Cook et al. 1971; Gaillard et al. 2000), so knowledge of fawn survival should increase understanding of the population ecology of deer in diverse landscapes.

My objectives were to estimate survival, assess cause-specific mortality and quantify space use of fawn white-tailed deer in an agro-forest ecosystem in south central Michigan. I estimated survival at 2- and 6-months postpartum to describe risks during the sedentary period of fawns and to allow comparison of my findings to other studies, respectively. I assessed cause-specific mortality for the same time periods to describe what mortality risks existed during development (0–2 months old) and during increased independence from the dam (e.g., increased movements during hunting season; 0–6 months old), respectively. I also estimated space use and cover selection to describe cover used by fawns during the first 2 months postpartum.

STUDY AREA

My study was conducted in eastern Jackson (Grass Lake, Henrietta, and Waterloo townships), western Washtenaw (Dexter, Lima, Lyndon, and Sylvan townships), and southwestern Livingston (Unadilla township) counties in the south central Lower Peninsula of Michigan (hereafter, Lower Michigan). The study area (82,636 ha) included publicly owned lands, including the Michigan Department of Natural Resources (MDNR) Waterloo (8,410 ha; 10.2% of study area) and Pinckney (4,276 ha; 5.2%) recreation areas, and privately owned lands. South central Michigan has been characterized by a relatively high deer density (~27/km^2 during fall 2005; MDNR 2005), increasing land-use activities (e.g., urbanization) and little scientific study of deer under these conditions. Although the study area was primarily rural (98% of total land area), the human population increased 16% and housing units increased 22% between 1990 and 2000 (U.S. Census Bureau 2003). Much of the landscape throughout southern Michigan (and in other areas throughout the Midwest) is expected to experience increasing land-use activities similar to the study area (Madill and Rustem 2001).

The physiographic regions of this area are Hillsdale-Lapeer Hilly Upland, South Central Rolling Plain, and Southeastern Rolling Plain (Sommers 1977:24) with alfisols as the major soil order (Sommers 1977:36). Surface formations in the study area are the result of glaciation and include all 4 types present within Michigan (moraine, till plain, outwash plain, and lacustrine plain; Sommers 1977:32). Elevation of the study area ranged approximately 180–300 m and consisted of relatively limited relief (Sommers 1977:26, 33). The study area received about 81 cm of precipitation annually during 1971–2000 (based on conditions in Chelsea, Michigan; Midwestern Regional Climate Center, Champaign, Illinois, USA), and had a 150-day growing season (i.e., the average annual accumulation of daily mean temperatures >5.6 °C), generally occurring from 10 May to 7 October (Sommers 1977:46, 49). During 1971–2000, average annual snowfall was 99.3 cm and mean monthly temperatures ranged from –5.4 °C (Jan.) to 21.8 °C (Jul.) in Jackson County (Midwestern Regional Climate Center, Champaign, Illinois, USA).

Before European settlement, southern Michigan forests consisted of oak (*Quercus* spp.) and hickory (*Carya* spp.) in well-drained soils and beech (*Fagus grandifolia*), elm (*Ulmus* spp.), maple (*Acer* spp.), and basswood (*Tilia americana*) in poorly drained soils

(Sommers 1977:17). Much of the study area is well suited for agriculture (Sommers 1977:38). Most crop agriculture in Jackson and Washtenaw counties (total area = 366,483 ha) is corn (37,840 ha) and soybean (34,200 ha) production, followed by hay (17,200 ha), winter wheat (7,970 ha) and oats (930 ha; Michigan Department of Agriculture 2002).

I generalized land-use, land-cover data (Michigan Center for Geographic Information 2001) using ArcView GIS v3.2 software (Environmental System Research Institute, Redlands, California, USA) and Spatial Analyst extension to define 13 cover types within the study area: agriculture (non-vegetated farmland, row crops, forage crops; 52.3% of study area); conifer (pines [*Pinus* spp.], other upland conifers; 1.5%); herbaceous openland (herbaceous vegetation with <25% woody cover; 2.9%); lowland deciduous forest (>60% composed of deciduous tree cover; 8.0%); lowland shrub (with >60% non-water cover; 9.9%); mixed wetland (floating aquatic vegetation, emergent wetland, mixed non-forest wetland; 3.1%); northern hardwood (>60% canopy cover of maple, beech, ash [*Fraxinus* spp.], cherry [*Prunus* spp.], birch [*Betula* spp.]; 2.3%); oak association (>60% canopy cover of oak; 1.6%); upland deciduous forest (>60% canopy cover of upland deciduous trees; 11.6%); upland shrub (>25% woody cover; <0.1%); urban (low and high intensity, roads, parks, golf courses; 2.8%); water (surface, flowing; 3.9%); and other (aspen [*Populus* spp.] association, orchards, bare ground; 0.1%). Patch size of cover types ranged from <1 ha to >11,000 ha (e.g., an agricultural matrix) and had a mean size of 29.2 ha. Consequently, generalization of spatial data may have excluded certain fine-scale landscape characteristics (e.g., hedgerows, roads) in some instances.

METHODS

The capture season for neonatal fawns was from mid-May to mid-June 2004–2006. I expected capture success to peak around 1 June and instances of fawns flushing to increase greatly after mid-June, thus reducing the ability for successful capture; fawns >2 weeks old generally start flushing when approached by humans (Carroll and Brown 1977). My technicians and I captured neonates either by hand or in a fish-landing net (0.5-m-diameter net, 2-m-long extendable handle). A group of 2–6 people systematically searched potential fawning habitat (e.g., areas transitioning from forest to wetland or grassy field) for neonates (Lund 1975, Ballard et al. 1999). Isolated adult females occasionally provided us with behavioral signs of a nearby neonatal fawn (e.g., a doe looking toward an area several times/min; Downing and McGinnes 1969).

I weighed, sexed, ear-tagged (Style 681; National Band and Tag, Newport, Kentucky, USA) and radiomarked each captured neonate. Captured neonates also were aged using hoof growth measurements (Haugen and Speake 1958). The mortality-sensing radio-transmitters (Model M4210; Advanced Telemetry Systems, Isanti, Minnesota, USA) had an expandable collar to allow for growth and were designed to drop off after 9–12 months for retrieval (see Diefenbach et al. 2003). Transmitters had a unique frequency within the 151-MHz range, a mass of 60 g, and an expected minimum battery life of 12 months. The precise-event transmitter option provided a time-of-mortality estimate within 30 min for a maximum of ~5 d post-mortality (i.e., 5 days of no transmitter movement). I used SYSTAT v11 (Systat Software, Inc., San Jose, California, USA) and ProStat v4.02 (Poly Software International, Inc., Pearl River, New York, USA) for my statistical analyses. Michigan State University's All-University Committee on

Animal Use and Care approved all capturing and handling procedures for my study (Application No. 01/04-006-00).

Survival and Cause-specific Mortality

My technicians and I monitored fawns daily for the first 30 days following capture and 2–5 times/week thereafter to estimate survival and assess cause-specific mortality. I used the Mayfield method (Mayfield 1961, 1975), as modified by Bunck and Pollock (1993) for censored individuals, to estimate survival of fawns during 2- and 6-month periods post-capture. Period survival was based on fates and exposure days during each period to estimate the daily survival rate, as I assumed daily survival would vary by time period. For analyses, I excluded any fawn that did not exceed a 7-day acclimation period following capture, but I also estimated survival without an acclimation period. Individuals were censored if I believed they were alive at the time of transmitter recovery (e.g., the break-away collar dropped, collection of field data concluded). I also performed a hazard analysis based on the probability of death (i.e., the number of individuals dying/number of individuals at risk) by weekly time periods for a total of 24 weeks (see Winterstein et al. 2001).

My assessment of cause-specific mortality of recovered carcasses was based on my field observations and the necropsies performed by a wildlife pathologist (MDNR Wildlife Disease Laboratory, East Lansing, Michigan, USA). I classified mortalities of individuals into 5 categories: canid- (coyote [*Canis latrans*], red fox [*Vulpes vulpes*], gray fox [*Urocyon cinereoargenteus*], or domestic dog [*C. lupus familiaris*]) kill, malnutrition, vehicle collision, hunter-harvest and unknown. If I did not have enough post-mortality evidence to ascribe cause with reasonable certainty (e.g., total consumption of the carcass), then I considered the cause of mortality to be unknown.

Space Use

I estimated locations of fawns 2–5 times/week using triangulation from telemetry signals (White and Garrott 1990). To increase the accuracy of habitat-use assessment, my technicians and I located fawns in a systematic manner during varying time schedules on a diel basis, with ≥ 1 nocturnal location/deer/week (Beyer and Haufler 1992), except during capture periods. I used a 3-element Yagi antenna (Advanced Telemetry Systems, Incorporated, Isanti, Minnesota, USA), portable radio receiver (Model R-1000, Communications Specialists, Incorporated, Orange, California, USA), handheld global positioning system (GPS) unit (Model GPS IV; GARMIN International, Incorporated, Olathe, Kansas, USA) and mirror-sighting compass to estimate bearings.

I used the program LOCATE III (Pacer, Truro, Nova Scotia, Canada) to estimate locations of fawns using triangulated data based on the maximum likelihood estimator (Lenth 1981*a*, *b*), as recommended by White and Garrott (1990) and Nams and Boutin (1991). I used Animal Movement extension in ArcView GIS v3.2 software (Environmental System Research Institute, Redlands, California, USA) to estimate 95% kernel home ranges and to quantify cover composition within home ranges using my cover-type classification system.

My description of fawn cover included only individuals with ≥ 30 locations (Seaman et al. 1999) and that survived ≥ 2-months post-capture. I assumed this time period approximated the age of fawns with low activity (Jackson et al. 1972), and consequently, avoidance of predators through cover selection. Fawns may also have selected cover for thermal properties, although I could not assess these specific selection strategies due to my spatial scale of study. Relationships between cover use (the mean proportion of each cover type within individual kernel home ranges) and availability (the proportion of each cover type within the study area) characterized cover selection indices (Ivlev 1961). I followed the equations of Strauss (1979) to estimate 95% confidence limits of selection indices.

RESULTS

My technicians and I observed 55 neonatal fawns during the capture seasons, and captured and radiomarked a total of 34 (2004 = 9, 2005 = 10, 2006 = 15). Capture effort averaged 25.0 observer-hr/radiomarked neonate, but effort decreased by year (2004 = 39.2, 2005 = 30.8, 2006 = 12.3). I pooled age ($\bar{x}$ = 7.2 d ± 0.2 SE, range = 4.9–10.3), weight ($\bar{x}$ = 4.6 kg ± 0.2 SE, range = 3.1–6.7) and sex (56% male) data for calculations. Throughout my analyses, I pooled fawns by sex and assumed behavioral differences were minimal or nonexistent between male and female fawns during the early stages of life (see Ozoga and Verme 1986).

Survival and Cause-specific Mortality

I pooled survival data for all 3 capture seasons (*n* = 32 fawns) because no single capture season sample size exceeded 20 individuals, a minimum value recommended by Hensler and Nichols (1981) based on the uncertainty resulting from small sample sizes. My survival analyses both included and excluded 2 radiomarked fawns that died during the acclimation period (<7 days post-capture). With an acclimation period, daily survival by period using the Mayfield method was 0.9965 (60 d) and 0.9978 (180 d), resulting in the survival probabilities of 0.81 (60 d; SE = 0.07) and 0.67 (180 d; SE = 0.08). Six of 32 fawns died during the first 60 days, while none were censored; 10 of 32 died during the first 180 days, while 3 were censored (2 break-away collars dropped at <180 d; 1 fawn was censored from survival analysis because a wildlife rehabilitator removed the individual from the field for an unknown injury). Without a 7-day acclimation period, 2 additional fawns were included in my survival analysis (*n* = 34; 60 d = 0.75, 95% CL = 0.61–0.90; 180 d = 0.62, 95% CL = 0.45–0.79), slightly reducing survival estimates.

Mortality from canids was the highest cause of mortality (3 of 34 fawns; mean age = 33.7 d) for fawns ≤ 60 days (Table 2.1). Fawns 60–180 days ($\bar{x}$ = 125.4) experienced relatively high mortalities from vehicle collisions (Table 2.1). Breakaway transmitters had an approximate life span of 1 year during my study, which was expected based on manufacturer specifications.

I pooled data and considered probability of death over time based on weekly estimates. During weeks 2–4, and approximately week 16, the probability of death peaked (0.50 and 0.35, respectively). The probability of death was minimal and constant during other time periods.

Space Use

Twenty-six of 34 radiomarked fawns survived ≥ 2 months post-capture and were available for space-use analysis (i.e., had ≥ 30 location estimates). Locations/fawn for the first 2 months averaged 37.5 (SE = 0.9). Because of small annual sample sizes, I pooled location data of fawns to assess space use. Fawns were radiomarked for an average of 203.8 days before being removed from the study (i.e., mortality, censored).

Approximately half of the fawns that lived to 2 months were captured in agriculture and upland deciduous forest cover types (Table 2.2). Home-range estimates averaged 40.9 ha and were highly variable (SE = 6.8; range = 2.7–166.8 ha) among fawns during their first 2 months. About 50% of the mean composition of home ranges included agricultural areas and conifers; no home ranges included the categories upland shrub and other, although each existed in very small proportions (~0.1%) on the study area. Only 2 cover types (conifer, lowland deciduous forest) were used in proportions greater than available, whereas 4 cover types (agriculture, herbaceous openland, other, upland shrub) were used less than expected; all other cover types (e.g., mixed wetland, northern hardwood) were neutrally used (i.e., CLs bracketed 0). Conifers were strongly selected for, and also comprised 26% of the mean home range area during the first 2 months.

DISCUSSION

Survival and Cause-specific Mortality

Relatively little published information is available describing demographics and cover types that provide cover specific to the first 2 months of life for white-tailed deer fawns. Vreeland et al. (2004) estimated 9-week survival of fawns at 72.4% (agricultural cover types) and 57.2% (forested cover types) in Pennsylvania, both lower than my estimate (81%). Eight-week-old fawns had low survival in a suburban environment in Alabama (33%; Saalfeld and Ditchkoff 2007). Pusateri Burroughs et al. (2006) estimated survival (Kaplan-Meier estimator; Winterstein et al. 2001) for each of 2 years at ≥90% (interpolated from fig.1) for 2-month-old fawns in southwestern Lower Michigan; my 180-day survival estimate (67%) was less than their 220-day lowest annual estimate (76%). Other survival estimates of fawns ≤2 months old included 90% (4 weeks post-capture, Minnesota; Brinkman et al. 2004), 89% (1–30 d, Massachusetts; Decker et al.

1992), 86% (<30 d) and 84% (<60 d, Iowa; Huegel et al. 1985), and 80% (0–30 d) and 100% (31–60 d, Mississippi; Bowman et al. 1998). Generally, published fawn survival estimates by time period were lowest earliest in life, similar to my results.

My survival estimates may be overestimated to some degree (assuming that radio-transmitters and capture did not affect survival; see Ozoga and Clute 1988), as mortality may be higher during the first several days postpartum (i.e., I discovered the remains of several dead unmarked neonates ≤ 1 week old on the study area). My radiomarked fawns had an estimated mean age of 7.2 days (SE = 0.2) at capture, also suggesting an overestimation of survival. When comparing survival estimates, spatial (e.g., vegetation structure) and temporal (e.g., weather patterns) differences should be considered. Pooling data over years, as I did, may result in some lost information (e.g., potential correlation between survival and weather), but may still provide a reasonably accurate mean survival estimate over time. Aspects related to timing of births, intragenerics (not present on my study area), and predation may greatly influence fawn survival (e.g., Whittaker and Lindzey 1999) within the geographic range of white-tailed deer, as well as the proportion of does in the study that are primiparous (Ozoga and Verme 1986). Survival estimates may also be influenced by the use of an acclimation period, although the use of such periods for neonate white-tailed deer has recently come into question (e.g., Carstensen Powell et al. 2005). Based on 95% CLs, an acclimation period made no difference in my survival estimates.

Because young fawns are sedentary, predation and malnutrition are often the causes of mortality, although I witnessed several fawns on or near paved roads. My data indicated that approximately 10% of fawns ≤2 months old were killed by predators (specifically, canids) and 3% died of malnutrition on my study area. Sixty-nine percent of fawn mortalities in southern Illinois were attributed to canids (Nelson and Woolf 1987); most of these fawns were 27–47 days, similar to my result ($\bar{x}$ = 34 d; Table 2.1). In 2 suburban areas in Chicago, Illinois, canids caused most (66% and 100%) mortalities of fawns between capture and 1 July (Piccolo 2002), whereas in suburban Alabama, 42% of mortalities of 8-week-old fawns were caused by canids (Saalfeld and Ditchkoff 2007). Huegel et al. (1985) found that almost 77% of fawn mortalities in Iowa were canid-related, with fawns <30 days seemingly most susceptible. Predation accounted for 67% of fawn mortality through a 12-week post-capture in southwest Minnesota, with 50% of predation attributed to coyotes and 50% unknown (Brinkman et al. 2004). At lower (e.g., Oklahoma, Bartush and Lewis 1981; Texas, Cook et al. 1971) and higher (e.g., New Brunswick, Canada, Ballard et al. 1999) latitudes, coyotes may also be the primary predator of fawns.

Before European settlement, coyotes existed primarily west of the Mississippi River, but currently their geographic distribution includes nearly all of the continental United States and Canada (Moore and Parker 1992). The increasing geographical distribution of coyotes may cause a change in deer demographics, especially in areas containing low-quality habitat for deer. Cause-specific mortality sources can be highly dependent on predator species and densities. No predator density estimates for canids (e.g., coyote, red fox) were available for my study area, but information from harvest surveys suggested an increasing trend in the relative abundance of coyotes in Michigan (D. Etter, MDNR, personal communication), which may influence the proportion of young fawns killed by predators.

The land-use changes on my study area included increasing urbanization; it would be logical to suspect that the number of domestic dogs increases and the proportion of available fawn cover decreases under these circumstances. Consequently, a potential increase in fawn depredation (or some level of compensatory shift in mortality) by canids seems likely if canid densities continue to increase, and some upper bound of urban development likely exists to reduce habitat suitability and negatively affect fawn survival (see Piccolo 2002). However, the effects that various levels of canid predation of fawns would have on deer population characteristics seem largely unknown.

Space Use

Although the relationship between survival and home-range composition may not be clear (e.g., Nixon and Etter 1995, Vreeland et al. 2004), and white-tailed deer can persist in a wide range of habitat conditions, I did have evidence of cover selection by 2-month-old fawns. Pusateri Burroughs et al. (2006) found cover selection (use) proportional to the composition of their Michigan study area (availability) for 27-week-old fawns. Cover selected on my study area consisted of conifers and lowland deciduous forests; however, home-range composition (ha) was highest for agricultural areas and conifers, respectively (Table 2.2). Although south central Texas had a different landscape composition than my study area, Carroll and Brown (1977) identified hiding cover of 2-month-old fawns at a fine spatial scale consisting of $\geq 70\%$ grasses, sedges, vines and forbs. Piccolo (2002) discussed the inverse relationship between hiding cover availability and risk to predation due to increased fawn movements where hiding cover is less available.

Fawn home-range sizes during my study were highly variable (2.7–166.8 ha). Although their analysis was for a period of 27 weeks, Pusateri Burroughs et al. (2006) also found a high variation in size (15.3–173.3 ha) of home ranges in southwestern Lower Michigan. In Michigan's Upper Peninsula, fawns occupied home ranges of 12.6 ha with little variation in size (range = 10.7–14.2) during the first 2 months, although the population studied was in a 252-ha enclosure containing a high deer population (≤ 107 deer; Ozoga et al. 1982). I found no other published results describing fawn space use during their first 2 months of life to make additional comparisons.

Although deer are often characterized as habitat generalists, the amount and quality of cover for fawns should have some relationship with survival. Additionally, because parturient and post-parturient female white-tailed deer are often territorial, and an age-related hierarchy may exist in white-tailed deer (Marchinton and Hirth 1984), a correlation between survival and cover types selected by fawns seems likely. The potential for fawn recruitment to affect deer population dynamics provides support for further study of this relationship. Certainly, high-quality habitat, by definition, would provide for reduced predation risk as a consequence of increased resource (i.e., food, cover) availability.

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Table 2.1. Fate assessment of fawn white-tailed deer (n = 34) during 0–60 and 0–180 days post-capture, south central Michigan, USA, 2004–2006.

Fate	Age (d) at assessment[a]	Proportion	
	$\bar{x}$ ± SE	≤ 60 d	≤ 180 d
Mortality			
Canid	33.7 ± 11.1	0.09	0.12
Malnutrition	15.4	0.03	0.03
Vehicle collision	125.4 ± 26.4	0.00	0.09
Hunter harvest	192.4 ± 5.5	0.00	0.03
Unknown	256.5 ± 240.7	0.03	0.03
Total	122.8 ± 33.0	0.15	0.30
Censored			
Dropped transmitter[b]	354.7 ± 54.6	0.00	0.06
End of study	233.2 ± 36.4	0.00	0.00
Other[c]	56.7 ± 49.8	0.06	0.09
Total	259.4 ± 34.3	0.06	0.15
Alive after time interval		0.79	0.55

[a] Age was defined as estimated age at capture plus accumulated days until fate was assessed.

[b] Fawns were radiomarked with break-away transmitters with an expected use of 9–12 months.

[c] Included mortality from capture stress and an injured fawn removed from study by a wildlife rehabilitator.

Table 2.2. Space use (95% kernel home ranges) description of radiomarked fawn white-tailed deer (n = 26) during approximately 0–2 months of age, south central Michigan, USA, May–July 2004–2006.

Cover type	Capture site[a] (p)	Presence in home range (p)	Home range composition (ha)		Selection index[b]	
			$\bar{x}$	SE	95% LCL	95% UCL
Agriculture	0.24	0.65	11.57	2.17	−0.31	−0.29
Conifer	0.15	0.46	10.77	3.87	0.73	1.00
Herbaceous openland	0.00	0.27	0.17	0.10	−0.99	−0.51
Lowland deciduous forest	0.18	0.65	5.08	1.58	0.07	0.36
Lowland shrub	0.06	0.62	3.55	1.10	−0.18	0.05
Mixed wetland	0.00	0.31	1.24	0.73	−0.70	0.68
Northern hardwood	0.06	0.65	2.37	0.70	−0.33	1.00
Oak association	0.03	0.15	0.59	0.45	−1.00	1.00
Upland deciduous forest	0.27	0.81	5.40	1.45	−0.03	0.16
Upland shrub	0.00	0.00	0.00			

Table 2.2. (cont'd).

Cover type	Capture site[a] (p)	Presence in home range (p)	Home range composition (ha)		Selection index[b]	
			$\bar{x}$	SE	95% LCL	95% UCL
	0.03	0.08	0.16	0.11	−1.00	−0.49
Urban						
	0.00	0.00	0.00			
Other						

[a] Included fawn mortalities that occurred >2 months post-capture ($n = 34$). Capture sites were recorded as UTM coordinates and cover-type assignment was made using a geographic information system describing land cover of the study area.

[b] Selection indices were based on Ivlev (1961), and include lower (LCL) and upper (UCL) confidence limits.

CHAPTER 3

A Multi-scale Approach to Describe Cover Selection of White-tailed Deer Using Use-Availability Data

A Multi-scale Approach to Describe Cover Selection of White-tailed Deer Using Use-Availability Data

INTRODUCTION

Selectivity, as described by Johnson (1980), relates to an animal's use of some resource (e.g., land-cover types) disproportionately to its availability; this assumes that resources selected in a proportion higher than their availability are more important than those resources selected against (i.e., "avoided", or proportional use < proportional availability). The assumption is that highly selected resources contribute positively to an animal's fitness (Garshelis 2000), with the obverse assumed true for highly avoided resources. But how availability is defined (e.g., spatial extent), including whether it is truly accessible to an individual or individuals, can impact how selection and avoidance are assigned (Buskirk and Millspaugh 2006). Also, as the defined spatial extent of availability is reduced (i.e., coarse to fine [landscape to home range] scale), selection may become more difficult to detect (McClean et al. 1998). Another potential problem is that different statistical techniques selected by researchers may provide different selection results (Garshelis 2000). "In many cases, interest will be in examining how habitat selection changes as availability changes" (Alldredge and Griswold 2006:337), which may provide insight into these potential problems.

By considering the hierarchical selection process used by organisms to meet their habitat requirements (Johnson 1980, Morrison et al. 1992), researchers can make inferences about habitat selection at multiple spatial scales; i.e., "the specification of habitat availability is equivalent to specification of a spatial scale at which to study the selection process" (Otis 1997:1016). Using a multi-scale approach while considering the natural history of an organism should improve our understanding of the ecology of that organism and lead to more informed and effective management decisions. For example, within a landscape, what coarse-scale features do white-tailed deer (*Odocoileus virginianus*) select (i.e., home-range characteristics), and what landscape features potentially affect population dynamics (e.g., avoidance of roads or urbanized areas, land-ownership patterns)? Within the home range, what habitat components do deer select (e.g., within-patch characteristics), and what is the relationship between these components and deer demographics (e.g., deer with adequate thermal cover have higher winter survival)? If we assume deer generally avoid urbanized areas within a landscape (coarse-scale approach), but deer exist locally in high densities within certain urbanized areas, then what are the differences in resource selection, movements, demographics, and cause-specific mortality between urban and rural areas? How should urban deer be managed differently from other deer populations? The patchy distribution of a species at various scales, from geographical distribution to metapopulation to family unit and finally, to individual, may be best examined by varying definitions of resource use and availability at different spatial scales. These definitions are, of course, human-derived.

Suggestions to reduce errors of assignment while conducting resource selection studies have been proposed, but often have not been implemented. For example, "researchers should consider studying selection at more than one scale" (Manly et al. 2002:5), but published research does not always address this consideration. Otis (1997) suggested that multi-scale approaches describing resource selection seemed to be becoming more prevalent; however, Thomas and Taylor (2006), in reviewing methods used in 87 papers in *The Journal of Wildlife Management* during 2000–2004, found that 57% considered only 1 spatial scale to assess resource selection. With highly specific research objectives, a single-scale study may be appropriate, however.

One potential method to address selection at various spatial scales is to vary the definitions of resource use and availability (Table 3.1). Challenges exist when defining resource availability; often, availability is most easily defined based on political boundaries or management units that may or may not consider ecological processes and animal movements. Defining study-area boundaries under these conditions may produce potentially spurious results depending on landscape-patch arrangement (Porter and Church 1987). Considering a multiple-scale approach would seem appropriate to provide support for management decisions based on selection.

My objectives were to quantify and compare cover selection of adult female white-tailed deer in south central Michigan at multiple spatial scales, and attempt to describe selection at multiple scales based on landscape-scale characteristics (e.g., patch size). My decision to use only adult females was related to describing relatively high-quality habitat for deer, as pooling age classes or considering only animal densities may confound issues related to habitat quality (Van Horne 1983), and therefore, resource selection. I assumed that habitat quality will be higher for adult deer than for juveniles because of a social dominance hierarchy (Marchinton and Hirth 1984), and that adult females may select areas with higher quality forage outside of the breeding season in comparison to males (Stewart et al. 2003). Further, evidence suggests that adult female white-tailed deer have higher reproductive success than juvenile females (e.g., Ozoga and Verme 1986, Mech and McRoberts 1990), and females are often the sex class of primary concern for managers desiring relatively large reductions in population densities through strategies such as hunter-harvest (Carpenter 2000).

STUDY AREA

My study was conducted in eastern Jackson (Grass Lake, Henrietta, and Waterloo townships), western Washtenaw (Dexter, Lima, Lyndon, and Sylvan townships), and southwestern Livingston (Unadilla township) counties in south central Lower Michigan. The study-area boundaries were defined specifically to include all townships containing ≥ 1 radiomarked deer location estimate, a method based on animal distribution suggested by McClean et al. (1998) and Erickson et al. (2001) to avoid the somewhat arbitrary definition of study-area boundaries. The study area (82,636 ha) included publicly owned lands (17.8% of study area), including the Michigan Department of Natural Resources (MDNR) Waterloo (8,410 ha; 10.2%) and Pinckney (4,276 ha; 5.2%) recreation areas, and privately owned lands (82.2%). South central Michigan has been characterized by an increase in urbanization and development, and a relatively high deer density (~27/km^2 during fall 2005; MDNR 2005). Little scientific information exists about deer under these landscape conditions. Although the study area was primarily rural (98% of total land area), the human population increased 16% and housing units increased 22% between 1990 and 2000 (U.S. Census Bureau 2003). Much of the landscape throughout southern Michigan (and in other areas throughout the Midwest) is expected to experience increasing land-use activities similar to the study area (Madill and Rustem 2001).

The physiographic regions of south central Michigan are Hillsdale-Lapeer Hilly Upland, South Central Rolling Plain, and Southeastern Rolling Plain (Sommers 1977:24) with alfisols as the major soil order (Sommers 1977:36). Surface formations in the study area are the result of glaciation and include all 4 types present within Michigan (moraine, till plain, outwash plain, and lacustrine plain; Sommers 1977:32). Elevation of the study area ranged from approximately 180 to 300 m and consisted of relatively limited relief (Sommers 1977:26, 33). The study area received about 81 cm of precipitation annually during 1971–2000 (based on conditions in Chelsea, Michigan; Midwestern Regional Climate Center, Champaign, Illinois, USA), and had a 150-day growing season (i.e., the average annual accumulation of daily mean temperatures >5.6° C), generally occurring from 10 May to 7 October (Sommers 1977:46, 49). During 1971–2000, average annual snowfall was 99.3 cm and mean monthly temperatures ranged from –5.4 °C (Jan) to 21.8 °C (Jul) in Jackson County (Midwestern Regional Climate Center, Champaign, Illinois, USA). Annual snowfall during my study was highly variable (2004 = 90.9 cm, 2005 = 149.9 cm, 2006 = 40.0 cm; Chelsea, Michigan; Midwestern Regional Climate Center, Champaign, Illinois, USA).

Before European settlement, southern Michigan forests consisted of oak (*Quercus* spp.) and hickory (*Carya* spp.) in well-drained soils and beech (*Fagus grandifolia*), elm (*Ulmus* spp.), maple (*Acer* spp.), and basswood (*Tilia americana*) in poorly drained soils (Sommers 1977:17). Much of the study area is well suited for agriculture (Sommers 1977:38). Most crop agriculture in Jackson and Washtenaw counties (total area = 366,483 ha) is corn (37,840 ha) and soybean (34,200 ha) production, followed by hay (17,200 ha), winter wheat (7,970 ha), and oats (930 ha; Michigan Department of Agriculture 2002).

I generalized land-use, land-cover data (Michigan Center for Geographic Information 2001) using ArcView GIS v3.2 software (Environmental System Research

Institute, Redlands, California, USA) and Spatial Analyst extension to define 13 primary cover types within the study area: agriculture (non-vegetated farmland, row crops, forage crops; 52.3% of study area); conifer (pines [*Pinus* spp.], other upland conifers; 1.5%); herbaceous openland (herbaceous vegetation with <25% woody cover; 2.9%); lowland deciduous forest (>60% composed of lowland deciduous tree cover; 8.0%); lowland shrub (with >60% non-water cover; 9.9%); mixed wetland (floating aquatic vegetation, emergent wetland, mixed non-forest wetland; 3.1%); northern hardwood (>60% canopy cover of maple, beech, ash [*Fraxinus* spp.], cherry [*Prunus* spp.], birch [*Betula* spp.]; 2.3%); oak association (>60% canopy cover of oak; 1.6%); upland deciduous forest (>60% canopy cover of upland deciduous trees; 11.6%); upland shrub (>25% woody cover; <0.1%); urban (low and high intensity, roads, parks, golf courses; 2.8%); water (surface, flowing; 3.9%); and other (aspen [*Populus* spp.] association, orchards, bare ground; 0.1%). Publicly owned lands had different proportions of cover types in relation to the study area (e.g., public lands have about twice the proportion of conifers and upland deciduous forests, but one-forth the proportion of agriculture). Patch size of cover types on the study area ranged from <1 ha to >11,000 ha (e.g., an agricultural matrix) and had a mean size of 29.2 ha (median = 4.7 ha). Consequently, generalization of spatial data may have excluded certain fine-scale landscape characteristics (e.g., hedgerows, roads) in some instances.

METHODS

Capturing Deer

Technicians and I trapped deer during winter (Dec–Mar) 2004–2006, using single-door live traps (Clover 1954). Traps were placed near areas of deer activity, baited with kernel corn, and checked twice/day to minimize stress and injury to deer. We restrained captured deer using the collapsed trap and the body weight of 1 person (Sparrowe and Springer 1970). All trapped deer were blindfolded to reduce stress and fitted with metal ear tags bearing a unique identification number (Style 681; National Band and Tag, Newport, Kentucky, USA). Individuals were aged as fawn (<1 year), yearling (≥ 1 year–<2 years), or adult (≥ 2 years) through general morphometric differences (e.g., shape and size of head, body size) and dental characteristics (Severinghaus 1949); ages of necropsied individuals later confirmed accuracy of field observations.

Only female deer were fitted with mortality-sensing collar-style radio-transmitters, either with VHF (Model 500; Telonics, Inc., Mesa, Arizona, USA) or VHF-GPS (Model G2000; Advanced Telemetry Systems, Isanti, Minnesota, USA) capabilities. I did not radiomark male deer because I expected low capture success for adult males based on previous trapping experience and deer behavior. Additionally, winter-captured male deer were not radiomarked because of potential problems associated with fitting a radio-transmitter to deer to accommodate their physiological changes (i.e., neck-swelling) during the breeding season. Radio-transmitters had a unique frequency within the 150-MHz range, a mass of 270 g (VHF) or 1,100 g (VHF-GPS), and an expected minimum battery life of 36 months (VHF) or 12 months (VHF-GPS). Michigan State University's All-University Committee on Animal Use and Care approved all capturing and handling procedures for my study (Application No. 01/04-006-00).

Estimating Locations

Deer locations were estimated 2–5 times/week using triangulation methods associated with telemetry (White and Garrott 1990) or from visual observations of known individuals. To increase the potential of my analyses to accurately describe cover-selection behavior, deer were located at varying time schedules in a systematic manner on a diel basis, with ≥ 1 nocturnal location/deer/week except during capture periods; for species (including deer) that potentially move at any time during a 24-hour period, "management recommendations developed from habitat use data collected from only a portion of a 24-hour period may be ineffective" (Beyer and Haufler 1992:180). Bearings were estimated using a 3-element folding Yagi antenna (Advanced Telemetry Systems, Incorporated, Isanti, Minnesota, USA), portable radio receiver (Model R-1000, Communications Specialists, Incorporated, Orange, California, USA), and mirror-sighting compass. A global positioning system (GPS) handheld unit (Model GPS IV; GARMIN International, Incorporated, Olathe, Kansas, USA) was used to approximate the locations from which signals were received.

Locations from triangulated data were estimated using the program LOCATE III (Pacer, Truro, Nova Scotia, Canada). I used the maximum likelihood estimator (Lenth 1981*a*,*b*), as recommended by White and Garrott (1990) and Nams and Boutin (1991). Bearing standard deviation and error ellipses were estimated using LOCATE III for each location during analysis. I based telemetry error assessments on the relationship between mean error-ellipse size and mean landscape-patch size to determine if I had appropriate sample sizes (see Nams 1989).

Cover Selection

Female deer that were captured as fawns or yearlings were reclassified as adults on either the first (for yearlings) or the second (for fawns) 1 June following their capture and subsequently used in my analyses. I assumed that all location estimates that were classified in the cover type water were inaccurate and I relocated each to the nearest alternative cover type. Cover selection was determined seasonally based on agricultural crop production (i.e., the growing season [150 d; 10 May–7 Oct], and the non-growing season [215 d; 8 Oct–9 May]) in the study area. I assumed these 2 time periods approximated seasonal differences in resource (e.g., food) availability and certain behaviors (e.g., parturition and primary fawn-rearing during the period of high food availability during the growing season, breeding and fasting during the period of low food availability during the non-growing season). Because there was low use of some cover types (e.g., proportional use of 6 of 13 cover types in 95% kernel home ranges during the growing season was <0.02), I did not consider compositional analysis as an appropriate method to describe resource selection (Thomas and Taylor 2006).

The hierarchical selection process proposed by Johnson (1980) described 4 resource selection scales, from coarse-scale (first-order selection: geographical range) to fine-scale (fourth-order selection: selection of particular food items at a site). This hierarchy describes a continuum of habitat selection, where first-order selection implies coarse-scale habitat requirements are present based on the geographic distribution of a species (e.g., a comparison of current and past land-cover conditions to describe the increase in distribution and abundance of deer [see McCabe and McCabe 1984]); fourth-order selection may describe fine-scale habitat components (e.g., characteristics of bedding sites selected by fawns; Huegel et al. 1986) that may contribute to increased fitness of an individual. Studies including intermediate orders of selection are perhaps the most common in wildlife science as a result of data collection methods and management objectives.

I described second- (e.g., home range selection within the study area) and third-order (e.g., cover selected within a home range) selection (Table 3.1) for deer, as my data were not appropriate to describe first- and fourth-orders of selection. I used SYSTAT v11 (Systat Software, Inc., San Jose, California, USA) for my data analyses and followed study designs 1–3 of Thomas and Taylor (1990) to describe cover selection processes of deer and the magnitude of their differences at different spatial scales. I assumed, for example, that if a cover type was highly selected at multiple spatial scales, then its relative importance to deer was higher than a cover type selected at 1 spatial scale; other factors may also affect cover selection, however, such as the distribution of hunters or availability of private and public land on the study area. Unless noted otherwise, I used 95% confidence limits (CLs; LCL = lower, UCL = upper) in my statistical analyses. The use of confidence limits is advantageous in that an estimate of effect size and a measure of uncertainty are provided (Johnson 1999).

Design 1: Population-level use and availability.—Use and availability under design 1 of Thomas and Taylor (1990) were quantified using Euclidean distances to define use and availability of cover types on my study area. Although this analysis method is most often used for linear or point features, it is equally valid for spatial features such as cover types (i.e., features described as polygons; Conner and Plowman 2001). I pooled all location data (i.e., individuals were not identified) and determined the

Euclidean distance between each location to each of the nearest cover types within my classification system. To describe availability, within the study-area boundaries I used 1,000 randomly generated points from a uniform distribution and measured Euclidean distances using methods identical to those used for location estimates.

Design 2: Individual use, population-level availability.—Use is estimated for each individual while availability for all individuals is identical under design 2, the seemingly dominant approach in selection studies (Thomas and Taylor 1990). I defined availability as the composition of cover types within the study-area boundaries and I used 95% fixed-kernel home ranges to assess selection under this study design. Kernel home ranges were estimated using the Animal Movement extension (Alaska Biological Sciences Center, Glacier Bay, Alaska, USA) in ArcView GIS v3.2 software. I used only deer with ≥30 locations/seasonal home range to describe cover selection (Seaman et al. 1999). I also estimated the amount of publicly owned land within seasonal home ranges. I used zero-intercept linear regression models to determine if there was a relationship between home-range size and amount of public land within home ranges.

The fixed-kernel method was chosen over other estimators for several reasons. First, the kernel methods (fixed and adaptive) met more criteria of importance (e.g., nonparametric estimation, sensitivity of outlying locations) than other home-range estimators (Kernohan et al. 2001:132–140). Secondly, the fixed-kernel method has lower bias when estimating the outer contours of the utilization distribution when compared to the adaptive-kernel method (Seaman et al. 1999). This is due to the smoothing parameter (h) being held constant with the fixed-kernel method as opposed to a variable h with the adaptive kernel method (i.e., a smaller h in areas of more dense utilization and a larger h

in areas with less dense utilization; Worton 1989, Powell 2000). I used the least-squares cross-validation method for smoothing-parameter selection (Worton 1995, Seaman et al. 1999).

Design 3: Individual use and availability.—Both use and availability are defined at the individual level with design 3 (Thomas and Taylor 1990). I defined use as the proportion of location estimates of an individual within each cover type, and availability as the proportional area of each cover type within the 95% kernel home range of that individual. Design 3 seems an appropriate measure of availability at finer spatial scales because kernel home ranges may overestimate the space used by an animal (i.e., cover types containing no location estimates are often included in a home-range estimate; Guthery et al. 2005). Consequently, I developed 2 methods to characterize availability of cover types within kernel home ranges: conditional and unconditional presence of cover types. Conditional analyses excluded cover types not present within an individual's home range, while unconditional analyses included all cover types within the study area for the estimation of selection indices.

Selection Indices.–I used Ivlev's (1961) electivity index as a measure of cover selection for each individual and calculated the mean for each cover type by season. This ratio provides an index ranging from −1 (implying avoidance; proportion used < proportion available) to 1 (implying selection; proportion used > proportion available), with 0 (proportion used = proportion available) suggesting random use. Confidence limits for Ivlev's index were truncated at −1 (LCL) or +1 (UCL) when appropriate. I compared selection within and among study designs based on the confidence limits of selection indices (see below) to investigate cover use by deer at multiple spatial scales.

Because point estimates alone may not provide an accurate estimate of resource selection (Hobbs and Bowden 1982), I based selection assignment (cover types selected, avoided, or randomly used) on confidence limits. Confidence limits were calculated using individuals as the sample unit (data were pooled by season so that a deer may have been included in ≥ 1 growing or ≥ 1 non-growing season). For design 1, confidence limits based on the means and standard errors of Euclidean distances were used to assign selection, but to compare selection with designs 2 and 3, I calculated Ivlev's electivity index based on ratios of mean Euclidean distances. Because using mean Euclidean distances as a ratio to assign selection results in mathematical signs opposite (i.e., negative values imply selection) to the results normally obtained using other analytical methods, I reversed the mathematical signs of the selection indices of design 1 to remain consistent with selection assignment under designs 2 and 3. For each cover type within each season under design 1, I assigned selection (used UCL < random LCL), avoidance (used LCL > random UCL), and random use (overlapping CLs) based on confidence limits of Euclidean distances.

I followed Strauss (1979) to estimate confidence limits of selection indices under designs 2 and 3. Under design 3, I assessed selection based on conditional and unconditional analyses; conditional analysis included only those cover types present within an individual's home range, while unconditional analysis included all 13 cover types (i.e., a non-represented cover type had a proportional availability = 0).

Ranking Cover Types.–I used Ivlev's electivity indices to rank selection both within and among study designs by season. This ranking method would probably be best described as a relative ranking system as opposed to an absolute rank of cover types (see

Johnson 1980). Specifically, "Absolute statements about preference or avoidance should be guarded against. Relative statements are possible because their nature invokes the concept of selection order" (Johnson 1980:69). Essentially, a relative ranking system does not make assignments of selection, avoidance, or random use for cover types, but rather ranks cover types based on selection index values. This may be advantageous when comparing indices derived from use-availability data collected or analyzed using different methods.

I ranked cover types within a study design and growing season by selection indices (i.e., the cover type with the highest selection index within a set received a rank of 1, and so on). Cover types with identical selection indices within a design and season were assigned identical ranks. To assess overall relative importance, I assigned the average rank ($\overline{R_i}$) among study designs for each cover type *i* within a season based on the equation

$$\overline{R}_i = [\text{design 1} + \text{design 2} + (0.5 \times \text{design 3U}) + (0.5 \times \text{design 3C}]/3,$$

which incorporated the weighted average of the 2 design 3 methods (U = unconditional, C = conditional). Ranking of cover types among designs was ordered from the lowest $\overline{R_i}$ (assigned the rank of 1) to the highest $\overline{R_i}$ (assigned the highest rank value within the set of cover types). Cover types with identical values of $\overline{R_i}$ were assigned the same rank. For example, if cover types 1 and 2 each had $\overline{R_i} = 5$ (i.e., $\overline{R_1} = \overline{R_2} = 5$), and there were 3 cover types with $\overline{R_i} < 5$, cover types 1 and 2 were both assigned the rank of 4; if cover type 3 had the next highest $\overline{R_i}$, it was assigned a rank of 6 because there were 5 cover types with $\overline{R_i} < \overline{R_3}$.

RESULTS

Capture and Estimation of Locations

I captured and radiomarked a total of 42 female deer during 3 winter seasons. A subset of 20 radiomarked deer that were either aged as adult during capture or that moved into the adult age class during the study was available for analysis (i.e., individuals with ≥ 30 locations; Seaman et al. 1999). This subset contained a total of 3,493 location estimates and a mean of 71 locations/seasonal home range. I pooled data by season but not by year due to small sample sizes. The growing seasons of 2004, 2005, and 2006 included 7, 14, and 3 deer, respectively. The non-growing seasons of 2004, 2005, and 2006 included 7, 11, and 7 deer respectively. Five deer were included in similar seasonal categories for >1 year.

I pooled location estimates (3,493) from all adult deer ($n = 20$) from my study to estimate overall telemetry error. I considered telemetry error acceptable, and thus, location estimates of acceptable precision, given the landscape characteristics of the study area (e.g., $\bar{x} = 29.2$ ha/patch), the mean telemetry error-ellipse size (10.2 ha), and the number of location estimates ($\bar{x} = 71$/deer). This conclusion was based on the relationship between telemetry error and patch size (diameter ratio = 0.59) to determine appropriate sample sizes as described by Nams (1989).

Cover Selection

Design 1: Population-level use and availability.—Under design 1, selection was assigned for 8 and 9 cover types for the growing and non-growing seasons, respectively (Table 3.2). Selection indices for both seasons ranked conifers and upland deciduous forests as the most highly selected (each $I > 0.40$), while agriculture was the most highly avoided cover type. Although indices differed somewhat between seasons, the patterns of selection were similar when assessed under this design (Table 3.3). Two cover types moved 1 rank value (lowland deciduous forest, other), while 1 cover type (oak association) moved from a rank of 8 during the growing season to a rank of 6 during the non-growing season. All other cover types were ranked consistently between seasons, suggesting no change in relative selection under this study design.

Design 2: Individual use, population-level availability.—The cover types upland shrub and other were absent (i.e., received no use) from kernel home ranges under design 2; consequently, I considered both as highly avoided cover types during both seasons (Table 3.4). Urban areas were the most highly avoided, but used, cover type during both seasons. Design 2 analysis assigned fewer cover types as selected (i.e., based on my definition of selection) in comparison to design 1. Conifers were highly selected, while lowland shrub and upland deciduous forest were moderately selected, with similar selection indices for all 3 cover types during both seasons. Ranking of cover types by season was similar under design 2 (Table 3.3). Herbaceous openlands and water each changed in their relative importance between seasons by a value of 2; herbaceous openlands became more important and water less important during the non-growing season. Although locations estimated to be in water were moved to the nearest alternative cover type, water was often included within kernel home-range boundaries.

When I plotted amount of public land within home ranges (ha) as a function of seasonal home-range size (ha), my models for both seasons showed a positive linear relationship. For the growing season, the relationship was described by $y = 0.54x$ (95% CL = 0.41–0.68 for x-coefficient; $r = 0.87$), while for the non-growing season, the relationship was $y = 0.52x$ (95% CL = 0.40–0.64; $r = 0.88$). Because 95% CLs overlapped for the x-coefficients, I pooled all data, which resulted in a relationship described by $y = 0.52x$ (95% CL = 0.44–0.61; $r = 0.87$; Fig. 3.2).

Design 3: Individual use and availability.—Unconditional analysis under design 3 assigned low but positive values for selection to 1 cover type during each season (upland deciduous forests for growing, conifers for non-growing; Table 3.5). All other cover types using conditional analysis were randomly used. The relative importance of cover types changed substantially between seasons (Table 3.3). Herbaceous openland, mixed wetland, and urban greatly decreased in importance (i.e., rank decreased ≥ 4) during the non-growing season; lowland shrub, oak association, and northern hardwood increased in importance (i.e., rank increased ≥ 3) during the non-growing season.

Similarly, under conditional analysis, proportional use was greater than proportional availability for upland deciduous forests (growing) and conifers (non-growing) under design 3; all other cover types were used randomly (Table 3.6). The difference in relative importance between seasons (growing minus non-growing) was greatest for urban (−9), oak association (+7), and mixed wetland (−4); moderate for herbaceous openland (−3), lowland shrub (+3), and northern hardwood (+3); all other cover types had a difference in rank of ≤ 2.

Ranking Cover Types.—Using my equation to estimate the mean rank among the study designs, most (77%) cover types had a similar rank between seasons (i.e., rank changed ≤ 1; Table 3.3). During the growing season, mixed wetland (+3) and urban (+2) increased in relative importance, while oak association decreased (−3) in relative importance. Conifers and upland deciduous forests were the 2 most important cover types irrespective of season, while agriculture, other, upland shrub, and urban generally were of low relative importance. Although use and availability of water were somewhat inconsistently defined among study designs, it seemed to have little effect on relative importance of cover types.

DISCUSSION

Garshelis (2000) discussed 2 assumptions relevant to selection studies, both seemingly related to human perception of resource selection by animals. How humans perceive resource availability could be different from how the species under study perceives availability (Litvaitis et al. 1996). Researchers may never fully understand these differences in perception, but this difference should be considered while designing studies (e.g., hierarchical selection process by animals [Johnson 1980]) and as a potential problem when interpreting results. Results that misrepresent the biology of an organism or the ecological processes throughout a landscape (e.g., vegetation succession) may lead to both cover assignment and management errors, especially under habitat manipulation strategies at the species level. If resource selection patterns emerge over multiple spatial scales, it would be logical to assume strong evidence exists for selection of certain resources. Conversely, depending on management objectives, we may question the efficacy of management decisions based on a single spatial scale, if that scale does not fit selection patterns.

The use of Johnson's (1980) system of ranking has been implemented in several ungulate studies. Lopez et al. (2004) used a multi-scale process (first-, second-, and third-order selection) to examine habitat use by Florida Key deer (*O. v. clavium*) in an increasingly urban environment; they found that Key deer generally selected for upland vegetation types regardless of spatial scale, and hypothesized that uplands provided preferred foods, cover, and freshwater. In Oregon, the relative importance of 11 plant communities were ranked and compared seasonally based on the feeding activities of mule deer (*O. hemionus*; individual animals were not identified) and the relative importance of each plant community varied substantially by season (Bodurtha et al. 1989:table 2). These examples provide evidence that resource selection studies should consider the selection behaviors and natural history of the species of interest. Failure to do so may provide an incomplete understanding of selection processes, resulting in less effective management.

Under the hierarchical selection process, selection at finer scales is dependent on selection at more coarse scales (Johnson 1980). To illustrate, third-order selection (e.g., the selection of conifers as thermal cover within a home range) is dependent on second-order selection (e.g., the selection of conifers across a landscape). My analyses showed strong patterns of selection regardless of spatial scale, but there were also some inconsistencies among certain cover types based on changes in their relative importance across multiple spatial scales. Conifers and upland deciduous forests were ranked as the 2 most important cover types on my study area regardless of the spatial (i.e., study design) or temporal (i.e., season) scale studied. Several cover types changed their relative importance across spatial scales. For example, during the growing season, urban areas shifted from unimportant at the landscape scale, but were increasingly important as a habitat component within home ranges; urban areas were unimportant during the non-growing season regardless of spatial scale. Deer near urban areas may have utilized these areas as fawning cover, although this is based on conjecture.

Single-scale Studies

I based my interpretation of selection patterns on past research, but white-tailed deer habitat is diverse across their geographic distribution, making comparisons somewhat difficult, especially as spatial scale decreases. Also, cover-type classifications are not consistent among studies, further increasing the difficulty of comparisons, especially across the geographic distribution of the white-tailed deer.

In Arkansas, Miranda and Porter (2003:table 1) used 2 general habitat suitability classes (food and cover) to model landscape-scale habitat suitability based on cover types. Although they did not specifically define cover, I assumed they primarily considered security as opposed to (winter) thermal cover given the mild climate of their study area. Their food and cover suitability values (an index of 0 to 1, with 0 being unsuitable) were both high for shrublands, deciduous forests, low-intensity residential, and woody wetlands; evergreen forests provided primarily cover, grassland-herbaceous and agricultural cover types provided primarily food; and water, high-intensity residential, and various other cover types were generally considered unsuitable. Although I found lowland shrubs to be relatively important during the non-growing season (Table 3.3), this cover type was not as important on my study area as suggested by Miranda and Porter (2003), and I believe that conifers (e.g., eastern redcedar [*Juniperus virginiana*]) on my study area contributed cover and some winter food value (see Bender and Haufler 1994) based on their relative importance (Table 3.3); the importance of upland deciduous forests (food and cover) on my study area seemed consistent with Miranda and Porter (2003) at the landscape level.

In Midwestern agricultural areas, white-tailed deer use agricultural crops throughout the year (Gladfelter 1984). Regardless of season, I found that agricultural areas increased in relative importance as spatial scale decreased (i.e., scale of selection became finer). This suggests that agricultural areas were much less important to deer at the landscape scale in comparison to providing a habitat component (food) within deer home ranges. This may explain why crop damage by deer seemed to be localized near field edges bordered by cover, at least for larger fields; smaller fields may have crop damage throughout (K. Bissell, MDNR, personal communication). Approximately half of the study area was composed of agricultural areas, which was probably at a much higher proportion than to provide optimal conditions (see Chapter 4), which reduced the relative importance of this cover type.

I estimated selection indices under design 2 using data from Pusateri (2003) for white-tailed deer ≥6 months old in southwestern Lower Michigan for comparison to my results. Cover types were defined differently for my study and data were not pooled by season. Cover-type compositions between study areas were similar, but mean patch size differed (20.3 ha for southwestern Michigan, 29.2 ha for my study), suggesting that other landscape characteristics (e.g., amount of edge) may also have been different between study areas. Kernel home ranges (ranked by Ivlev's electivity index) included the cover types evergreen forest (0.64), emergent herbaceous wetland (0.55), woody wetland (0.23), deciduous forest (0.20), and agriculture (−0.16); all other cover types were not used by deer. The only strong similarity between Pusateri (2003) and my study was the relative importance of conifers (evergreen forests), although deciduous forests also comprised a large portion (47%) of kernel home ranges (i.e., proportional use) for

Pusateri (2003) and my study (~28% during each season). Wetland cover types seemed to have a higher relative importance to deer in southwestern Michigan than in my study.

Issues of Scale

Cover selection of deer on my study area showed scale effects. From coarse to fine scale, or as the spatial extent of availability declined, fewer cover types were assigned as selected (i.e., proportional use > proportional availability), similar to McClean et al. (1998). Eight cover types were assigned as selected under design 1 (landscape scale), while 3 were assigned as selected under design 2 (meso-scale), and 2 for each variant of design 3 (fine scale). My landscape-scale definition of availability encompassed the entire study area. Movements of individual radiomarked deer on my study area were limited to much smaller areas than the entire study area, suggesting that resource availability may have been overestimated.

Design 2 and design 3 (conditional and unconditional) seemed most appropriate to describe cover selection by deer on my study area, as selection was fairly consistent among designs. Considering our biological knowledge of white-tailed deer, these designs supported my expectations of cover use by deer. For example, under design 2, conifers, lowland shrubs, and upland deciduous forests were selected regardless of season, perhaps as a result of the proximity of cover types. Under each variant of design 3, conifers were selected during the non-growing season and upland deciduous forests were selected during the growing season.

Human perceptions of wildlife cover selection, as defined through use and availability, may also be affected by landscape characteristics. For example, landscape characteristics (e.g., patch size, shape, and distribution across a landscape) probably affect the distribution of wildlife species, such as white-tailed deer, in a given area (Porter and Church 1987). The landscape matrix of my study area consisted of few large patches (i.e., >120 ha) of agricultural areas (i.e., too few to be identified by frequency in Fig. 3.1), which probably were in excess quantity relative to the space-use needs of white-tailed deer (see Chapter 4). Consequently, at the landscape scale, deer likely avoided large patches of agriculture. Given that publicly owned areas had about 25% of the proportion of agriculture (and twice the proportions of conifers and upland deciduous forests) than privately owned lands, habitat quality for deer may be higher on public lands in the study area. However, home-range size did not seem to decrease with increasing amounts of public land (Fig. 3.2), suggesting that parcel sizes of or the patches within public land may have been too small to reduce deer movements.

Conclusions

I used use-availability data of white-tailed deer to illustrate how and why a multi-scale approach (i.e., various methods describing use and availability) can be used to describe cover selection. If, for example, managers considered selection only under design 1, they might underestimate the importance of lowland deciduous forest (Table 3.3) when managing for white-tailed deer. Similarly, the oak association cover type may show no difference in relative importance between seasons (under design 2), but the relative importance as defined through a multi-scale analysis could show a large difference among spatial scales (Table 3.3) that may not otherwise be considered.

"Inference of selection patterns is limited to the scale designated by the researcher" (Erickson et al. 2001:217). Vreeland et al. (2004:542) found no relationship between home-range characteristics and survival of fawns in Pennsylvania, but mentioned that, "future studies should consider landscape-related characteristics on fawn survival," suggesting that a more coarse spatial scale (i.e., describing landscape characteristics such as patch size and juxtaposition) may have been more appropriate; interestingly, Erickson et al. (2001) suggested that generalist species, which white-tailed deer seem to be, might select resources at spatial scales finer than the landscape level. These seemingly contradictory statements seem to support the multi-scale resource selection approach for determining the appropriate spatial scale or scales of study.

I suggest using multiple spatial scales when assessing resource selection, assuming appropriate use-availability data were collected. This should improve the interpretation of resource selection analyses through stronger evidence of selection or avoidance through a comprehensive description of cover use. When researchers are unsure of the appropriate scale of study for an application, they may do well using a multi-scale selection analysis, ranking cover according to relative importance, then averaging the rank values as I have done. Relative importance of cover types across multiple scales should provide insight into cover selection, and therefore value of cover, for habitat management. Errors of assignment (e.g., effects of inappropriately defined resource availability) may also be minimized and overall selection patterns should emerge through such an approach.

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Table 3.1. Study designs (and definitions of use and availability in my study) for collection of use-availability data as described by Thomas and Taylor (1990, 2006) and Erickson et al. (2001), and selection hierarchy as defined by Johnson (1980).

	Scale and Definition		Selection
Study design	Use	Availability	Hierarchy
1	Population-level (study area)	Population-level (study area)	Second-order
2	Individual (kernel home range)	Population-level (study area)	Second-order
3	Individual (location estimates)	Individual (kernel home range)	Third-order
4[a]	Individual (location estimate)	Individual (paired with and defined for each use)	Fourth-order

[a]Study included designs 1–3; my use-availability data did not seem appropriate under study design 4.

Table 3.2. Cover selection of white-tailed deer ($n = 20$) based on Euclidean distances (95% confidence limits [m]; LCL = lower, UCL = upper) between cover types and location estimates or randomly generated points (1,000) within the study area, under design 1[a] of Thomas and Taylor (1990), south central Michigan, 2004–2006. Location estimates were pooled by agricultural growing season (1,626 locations for growing [10 May–7 Oct], 1,867 locations for non-growing season [8 Oct–9 May]).

			Season					
	Random		Growing			Non-growing		
Cover type	LCL	UCL	LCL	UCL	*I*	LCL	UCL	*I*
Agriculture	137.8	175.7	402.1	440.5	−0.39	320.8	351.2	−0.29
Conifer	1,549.9	1,720.5	487.0	554.6	0.47	454.4	515.6	0.50
Herbaceous openland	682.1	745.1	650.3	688.3	0.00	637.8	669.6	0.01
Lowland deciduous forest	357.2	395.8	353.9	381.8	0.00	371.2	394.8	0.00
Lowland shrub	398.4	459.3	229.0	251.7	0.23	233.7	256.5	0.22
Mixed wetland	1,321.4	1,476.1	585.9	634.8	0.35	652.6	696.3	0.31
Northern hardwood	712.1	792.6	355.4	377.5	0.31	367.5	386.8	0.30
Oak association	839.3	918.3	513.0	544.4	0.21	505.7	534.5	0.22

Table 3.2. (cont'd)

			Season					
	Random		Growing			Non-growing		
Cover type	LCL	UCL	LCL	UCL	I^a	LCL	UCL	I
Upland deciduous forest	355.7	402.8	122.6	138.3	0.44	133.7	148.6	0.41
Upland shrub	10,914.0	11,497.3	13,502.5	13,726.0	−0.08	13,167.8	13,367.3	−0.07
Urban	1,241.0	1,349.1	1,870.1	1,995.4	−0.16	2,000.7	2,108.3	−0.19
Water	1,726.8	1,905.9	870.1	953.1	0.29	1,007.6	1,077.5	0.23
Other	4,192.0	4,489.5	3,807.9	4,014.1	0.22	3,574.2	3,768.1	0.05

[a] Design 1 identifies population-level use and population-level availability. Individuals are not identified.

[b] Selection indices based on Ivlev's (1961) electivity index using mean distance of random points (availability) and used points (use). If 95% CLs overlapped, $I = 0.00$; if CLs of random points > CLs of used points, I was calculated using LCL of random and UCL of used ($I > 0$, implying selection); if CLs of random points < CLs of used points, I was calculated using LCL of used and UCL of random ($I < 0$, implying avoidance). Direction of index (+, −) shown is opposite of direction calculated (e.g., used mean distance > random mean distance would result in an index suggesting selection, but in reality implies avoidance).

Table 3.3. Relative importance of cover types by adult female white-tailed deer (*n* = 20) based on selection indices under multiple study designs (see Thomas and Taylor [1990]), south central Michigan, 2004–2006. Data were pooled by agricultural growing season (growing [10 May–7 Oct], non-growing [8 Oct–9 May]).

Season	Study Design[a]				Relative Importance[d]
Cover type	1	2	3U[b]	3C[c]	
Growing					
Agriculture	13	9	7	7	11
Conifer	1	1	2	3	1
Herbaceous openland	9	10	5	6	8
Lowland deciduous forest	9	6	3	4	6
Lowland shrub	6	3	7	8	4
Mixed wetland	3	7	3	4	3
Northern hardwood	4	4	10	10	5
Oak association	8	5	9	9	7
Upland deciduous forest	2	2	1	2	2
Upland shrub	11	12	11	11	13
Urban	12	11	5	1	10
Water	5	8	11	12	8
Other	7	12	11	12	12
Non-growing					
Agriculture	13	9	6	6	10

Table 3.3. (cont'd)

Season Cover type	Study Design[a] 1	2	3U[b]	3C[c]	Relative Importance[d]
Non-growing					
Conifer	1	1	1	1	1
Herbaceous openland	9	8	9	9	9
Lowland deciduous forest	10	6	3	4	7
Lowland shrub	6	3	3	5	3
Mixed wetland	3	7	8	8	6
Northern hardwood	4	4	7	7	5
Oak association	6	5	5	2	4
Upland deciduous forest	2	2	2	2	2
Upland shrub	11	12	10	10	12
Urban	12	11	10	10	12
Water	5	10	10	10	8
Other	8	12	10	10	11

[a] Designs are based on various definitions of use and availability described in text.

[b] Unconditional analyses included all cover types within the study area for describing selection.

[c] Conditional analyses excluded cover types not present within an individual's home range.

[d] Relative importance ($\overline{R}$) = [design 1 + design 2 + (0.5 × design 3U) + (0.5 × design 3C]/3; values shown are ranks based on these values.

Table 3.4. Cover selection of female adult white-tailed deer (n = 20) under design 2[a] of Thomas and Taylor (1990), south central Michigan, 2004–2006. Data were pooled by agricultural growing season (150 d; 10 May–7 Oct; 23 growing, 25 non-growing) within an agro-forest ecosystem.

Season Cover type	Presence in home range (p)	Proportional use		Selection index[b]			
		p	SE(p)	I	LCL[c]	UCL	Use[d]
Growing							
Agriculture	0.74	0.164	0.047	−0.52	−0.53	−0.51	−
Conifer	0.65	0.154	0.057	0.81	0.31	1.00	+
Herbaceous openland	0.22	0.009	0.007	−0.53	−1.00	0.17	o
Lowland deciduous forest	0.74	0.078	0.024	−0.02	−0.26	0.22	o
Lowland shrub	0.83	0.204	0.038	0.35	0.21	0.48	+
Mixed wetland	0.48	0.022	0.013	−0.17	−1.00	0.82	o
Northern hardwood	0.74	0.045	0.012	0.33	−1.00	1.00	o
Oak association	0.57	0.019	0.007	0.10	−1.00	1.00	o

Table 3.4. (cont'd)

Season Cover type	Presence in home range (*p*)	Proportional use[a]		Selection index[b]			
		p	SE(*p*)	*I*	LCL[c]	UCL	Use[d]
Growing							
Upland deciduous forest	0.96	0.288	0.044	0.43	0.33	0.52	+
Upland shrub	0.00	0.000		−1.00			−
Urban	0.09	0.002	0.001	−0.87	−1.00	−0.67	−
Water	0.48	0.015	0.005	−0.44	−0.99	0.11	o
Other	0.00	0.000		−1.00			−
Non-growing							
Agriculture	0.88	0.172	0.033	−0.50	−0.51	−0.49	−
Conifer	0.84	0.162	0.051	0.83	0.35	1.00	+
Herbaceous openland	0.40	0.012	0.006	−0.42	−1.00	0.44	o
Lowland deciduous forest	0.80	0.072	0.019	−0.06	−0.29	0.19	o

Table 3.4. (cont'd)

Season Cover type	Presence in home range (p)	Proportional use[a]		Selection index[b]			
		p	SE(p)	I	LCL[c]	UCL	Use[d]
Non-growing							
Lowland shrub	0.84	0.205	0.039	0.35	0.21	0.49	+
Mixed wetland	0.60	0.027	0.011	−0.07	−1.00	0.95	o
Northern hardwood	0.84	0.033	0.009	0.18	−1.00	1.00	o
Oak association	0.72	0.022	0.007	0.17	−1.00	1.00	o
Upland deciduous forest	1.00	0.282	0.035	0.42	0.32	0.51	+
Upland shrub	0.00	0.000		−1.00			−
Urban	0.08	0.001	0.001	−0.93	−1.00	−0.84	−
Water	0.40	0.012	0.004	−0.53	−1.00	−0.05	−
Other	0.00	0.000		−1.00			−

[a] Design 2 use was based on cover types bounded by 95% fixed kernel home ranges; availability was based on cover types bounded by the study area.

[b] Selection indices based on Ivlev's (1961) electivity index (*I*).

[c] Confidence limits (95%) were truncated at −1 and 1, and could not be estimated if proportional use = 0.

[d] If 95% CLs >0, selection (+) was assigned; if 95% CLs <0, avoidance (−) was assigned; and if 95% CLs included 0, random use (o) was assigned.

Table 3.5. Cover selection of female adult white-tailed deer (*n* = 20; design 3[a] of Thomas and Taylor [1990]) pooled by agricultural growing season (150 d; 10 May–7 Oct; 23 growing, 25 non-growing) in an agro-forest ecosystem in south central Michigan, 2004–2006. Proportional use and selection indices were unconditional on presence of cover types within home ranges.

Season	Proportional use		Selection index[b]			
Cover type	*p*	SE(*p*)	*I*	LCL[c]	UCL	Use[d]
Growing						
Agriculture	0.154	0.046	−0.03	−0.12	0.05	o
Conifer	0.168	0.063	0.04	−0.05	0.14	o
Herbaceous openland	0.009	0.008	0.00	−1.00	1.00	o
Lowland deciduous forest	0.081	0.026	0.02	−0.23	0.27	o
Lowland shrub	0.191	0.041	−0.03	−0.10	0.03	o
Mixed wetland	0.023	0.015	0.02	−1.00	1.00	o
Northern hardwood	0.030	0.009	−0.20	−0.76	0.36	o
Oak association	0.016	0.006	−0.09	−1.00	1.00	o
Upland deciduous forest	0.325	0.057	0.06	0.02	0.10	+
Upland shrub	0.000					
Urban	0.002	0.002	0.00	−1.00	1.00	o
Water	0.000					
Other	0.000					

Table 3.5. (cont'd)

Season	Proportional use[a]		Selection index[b]			
Cover type	*p*	SE(*p*)	*I*	LCL[c]	UCL	Use[d]
Non-growing						
Agriculture	0.162	0.038	−0.03	−0.11	0.05	o
Conifer	0.192	0.058	0.08	0.01	0.17	+
Herbaceous openland	0.005	0.004	−0.41	−1.00	1.00	o
Lowland deciduous forest	0.074	0.025	0.01	−0.27	0.30	o
Lowland shrub	0.206	0.042	0.01	−0.06	0.06	o
Mixed wetland	0.018	0.009	−0.20	−1.00	1.00	o
Northern hardwood	0.026	0.012	−0.11	−1.00	0.80	o
Oak association	0.022	0.011	0.00	−1.00	1.00	o
Upland deciduous forest	0.294	0.046	0.02	−0.02	0.06	o
Upland shrub	0.000					
Urban	0.001					
Water	0.000					
Other	0.000					

[a] Design 3 use was based on proportion of locations in each cover type averaged over individuals; availability was based on mean proportion of area of cover types bounded by individual 95% fixed kernel home range by season. Cover types absent from a home range had proportional availability = 0.

[b] Selection indices based on Ivlev's (1961) electivity index (*I*).

[c] Confidence limits (95%) were truncated at −1 and 1, and could not be estimated if proportional use = 0.

[d] If 95% CLs >0, selection (+) was assigned; if 95% CLs <0, avoidance (−) was assigned; and if 95% CLs included 0, random use (o) was assigned.

Table 3.6. Cover selection of female adult white-tailed deer (n = 20; design 3[a] of Thomas and Taylor [1990]) pooled by agricultural growing season (150 d; 10 May–7 Oct; 23 growing, 25 non-growing) in an agro-forest ecosystem in south central Michigan, 2004–2006. Proportional use and selection indices were conditional on presence of cover type within home ranges.

Season	Proportional use		Selection index[b]			
Cover type	p	SE(p)	I	LCL[c]	UCL	Use[d]
Growing						
Agriculture	0.209	0.062	−0.03	−0.10	0.04	o
Conifer	0.258	0.089	0.04	−0.03	0.12	o
Herbaceous openland	0.043	0.036	0.00	−1.00	1.00	o
Lowland deciduous forest	0.109	0.033	0.01	−0.20	0.22	o
Lowland shrub	0.230	0.044	−0.04	−0.09	0.02	o
Mixed wetland	0.048	0.030	0.01	−1.00	1.00	o
Northern hardwood	0.041	0.012	−0.20	−0.65	0.26	o
Oak association	0.028	0.009	−0.08	−1.00	1.00	o
Upland deciduous forest	0.339	0.058	0.06	0.03	0.09	+
Upland shrub						
Urban	0.026	0.026	0.18	−1.00	1.00	o
Water	0.000					
Other						

Table 3.6. (cont'd)

Season Cover type	Proportional use[a] p	 SE(p)	Selection index[b] I	 LCL[c]	 UCL	 Use[d]
Non-growing						
Agriculture	0.183	0.041	−0.03	−0.09	0.03	o
Conifer	0.228	0.067	0.08	0.02	0.14	+
Herbaceous openland	0.013	0.009	−0.38	−1.00	1.00	o
Lowland deciduous forest	0.091	0.030	0.01	−0.20	0.21	o
Lowland shrub	0.245	0.046	0.00	−0.04	0.05	o
Mixed wetland	0.029	0.014	−0.22	−1.00	0.64	o
Northern hardwood	0.031	0.014	−0.11	−0.77	0.55	o
Oak association	0.031	0.015	0.02	−1.00	1.00	o
Upland deciduous forest	0.294	0.046	0.02	−0.01	0.05	o
Upland shrub						
Urban	0.00					
Water	0.00					
Other						

[a]Design 3 use was based on proportion of locations in each cover type averaged over individuals; availability was based on mean proportion of area of cover types bounded by individual 95% fixed kernel home range by season. Cover types absent from a home range were not considered available to respective individual.

[b]Selection indices based on Ivlev's (1961) electivity index (*I*).

[c] Confidence limits (95%) were truncated at −1 and 1, and could not be estimated if proportional use = 0.

[d] If 95% CLs >0, selection (+) was assigned; if 95% CLs <0, avoidance (−) was assigned; and if 95% CLs included 0, random use (o) was assigned.

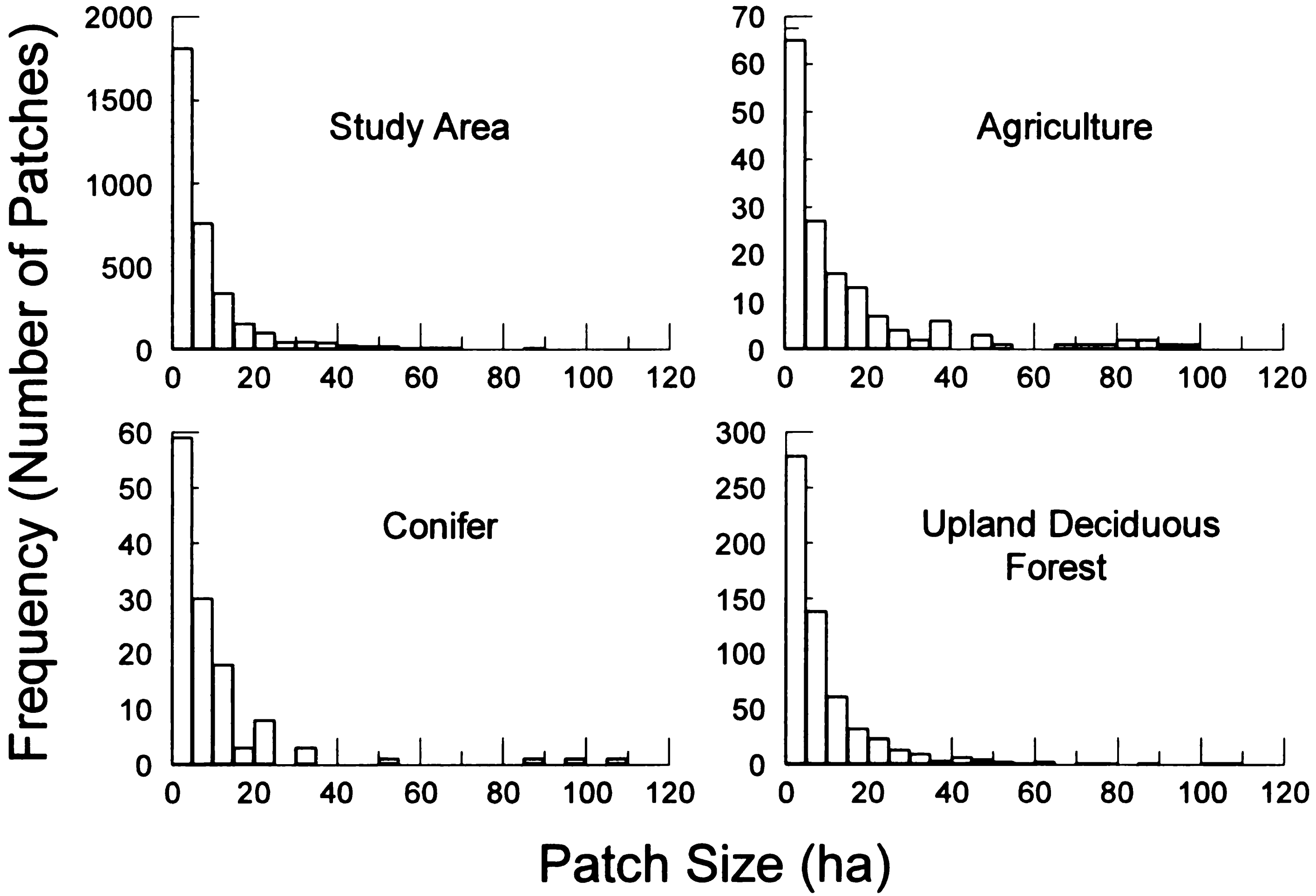

Figure 3.1. Frequency distribution of landscape-patch size (ha) for all 13 cover types on the study area, agricultural areas, conifers, and upland deciduous forests, south central Michigan, USA, 2004–2006.

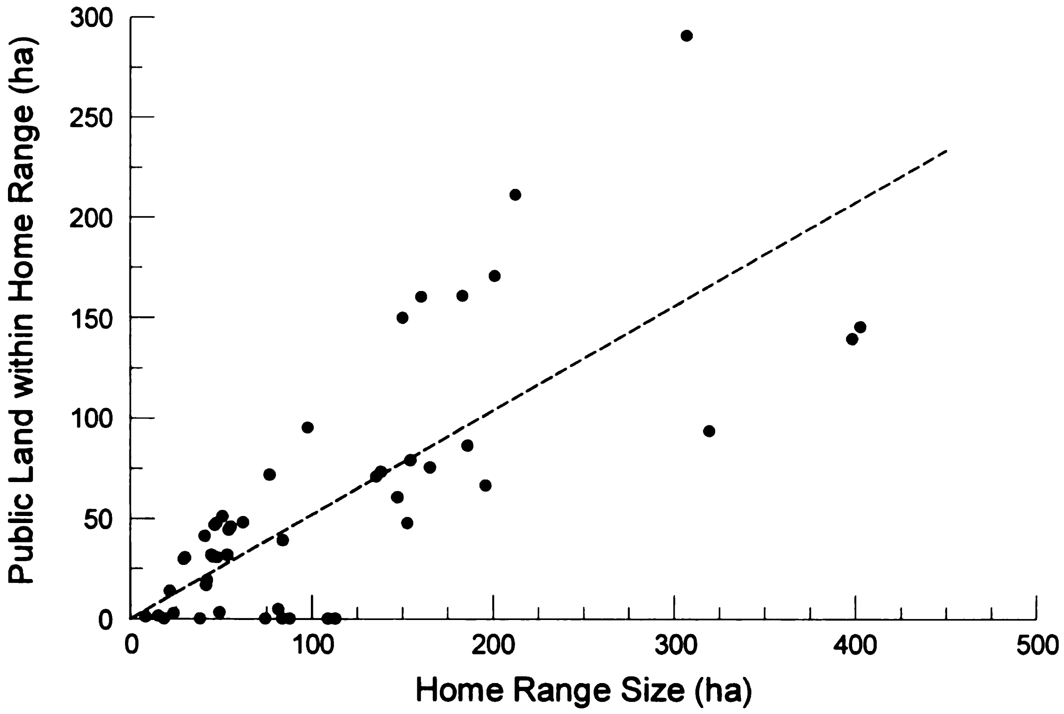

Figure 3.2. Linear relationship (*y* = 0.52x; *r* = 0.87; dashed line) of amount of public land within home range (ha) as a function of seasonal home-range size (ha) of adult female white-tailed deer (*n* = 20), south central Michigan, USA, 2004–2006. Seasonal home-range estimates were pooled and based on agricultural growing season (10 May–7 Oct for growing season, 8 Oct–9 May for non-growing season).

CHAPTER 4

Estimation and Implications of Space Use for White-tailed Deer Management in Southern Michigan

Estimation and Implications of Space Use for White-tailed Deer Management in Southern Michigan

INTRODUCTION

Habitat manipulation and harvest strategies are 2 primary management tools used to influence deer population size and distribution. Understanding space use by white-tailed deer (*Odocoileus virginianus*) is integral to successful habitat management strategies. McCullough (1987:547), in fact, stated, "Deer can be benefitted readily by habitat manipulation over most of their range, and there can be no question that habitat management is the keystone to continuing high populations." However, the success of any habitat management plan depends on the incorporation of accurate and appropriate scientific evidence. Managers can apply habitat management practices grounded in science as opposed to dogma for higher expectations of success.

Habitat management (e.g., land-cover conversions, altering current vegetation successional stages) is often done to change or redistribute the abundance of a particular species, although the effects of management on other wildlife species should be considered. Habitat manipulation can impact wildlife populations at different spatial scales, depending on the size, shape, frequency, and intensity of the manipulation or disturbance. For example, it may be possible to redistribute the individual animals on a managed area without affecting the overall abundance of that species by manipulating resources (food, water, cover), particularly those resources that are considered limiting. The conversion or redistribution of winter thermal cover (i.e., coniferous forest stands), a life requisite in northern latitudes (Ozoga 1968, Demarais et al. 2000), could theoretically influence deer behavior and demographics and redistribute deer densities.

With deer and human populations both generally increasing during the past several decades (McShea et al. 1997), wildlife managers face an increasingly challenging scenario. Urban and urbanizing areas may impose certain obvious control problems related to harvest management and habitat manipulation; at times, habitat manipulation may be the only option for deer management, as the harvest of deer in urban areas may be socially unacceptable or unsafe. Regardless, management options can become quite limited under these circumstances. These increasing challenges are the impetus behind integrating research with management, including space-use information specifically addressing issues of deer management in urbanizing areas.

My objectives were to quantify space use of white-tailed deer in an increasingly urbanizing agro-forest ecosystem in south central Michigan, to compare kernel home range estimates with usable space estimates, and to discuss the implications of cover conversions designed to increase or decrease the amount of suitable habitat for deer. I also developed some general rules of cover interspersion for habitat management of white-tailed deer based on my space-use assessments. In theory, an increase in habitat quantity or quality will increase the density or abundance of deer, with the obverse relationship also assumed to be true.

STUDY AREA

My study took place in eastern Jackson (Grass Lake, Henrietta, and Waterloo townships), western Washtenaw (Dexter, Lima, Lyndon, and Sylvan townships), and southwestern Livingston (Unadilla township) counties in south central Lower Michigan.

The study area (82,636 ha) included publicly owned lands, including the Michigan Department of Natural Resources (MDNR) Waterloo (8,410 ha; 10.2% of study area) and Pinckney (4,276 ha; 5.2%) recreation areas, and privately owned lands. South central Michigan has been characterized by a relatively high deer density (~27/km^2 during fall 2005; MDNR 2005), increasing land-use activities (e.g., urbanization), and little scientific study of deer under these conditions. Although the study area was primarily rural (98% of total land area), the human population increased 16% and housing units increased 22% between 1990 and 2000 (U.S. Census Bureau 2003). Much of the landscape throughout southern Michigan (and in other areas throughout the Midwest) is expected to experience increasing land-use activities similar to the study area (Madill and Rustem 2001).

The physiographic regions of this area are Hillsdale-Lapeer Hilly Upland, South Central Rolling Plain, and Southeastern Rolling Plain (Sommers 1977:24) with alfisols as the major soil order (Sommers 1977:36). Surface formations in the study area are the result of glaciation and include all 4 types present within Michigan (moraine, till plain, outwash plain, and lacustrine plain; Sommers 1977:32). Elevation of the study area ranged approximately 180–300 m and consisted of relatively limited relief (Sommers 1977:26, 33). The study area received about 81 cm of precipitation annually during 1971–2000 (based on conditions in Chelsea, Michigan; Midwestern Regional Climate Center, Champaign, Illinois, USA), and had a 150-day growing season (i.e., the average annual accumulation of daily mean temperatures >5.6 °C), generally occurring from 10 May to 7 October (Sommers 1977:46, 49). During 1971–2000, average annual snowfall was 99.3 cm and mean monthly temperatures ranged from –5.4 °C (Jan) to 21.8 °C (Jul) in Jackson County (Midwestern Regional Climate Center, Champaign, Illinois, USA). Annual snowfall during my study was highly variable (2004 = 90.9 cm, 2005 = 149.9 cm, 2006 = 40.0 cm; Chelsea, Michigan; Midwestern Regional Climate Center, Champaign, Illinois, USA).

Before European settlement, southern Michigan forests consisted of oak (*Quercus* spp.) and hickory (*Carya* spp.) in well-drained soils and beech (*Fagus grandifolia*), elm (*Ulmus* spp.), maple (*Acer* spp.), and basswood (*Tilia americana*) in poorly drained soils (Sommers 1977:17). Much of the study area is well suited for agriculture (Sommers 1977:38). Most crop agriculture in Jackson and Washtenaw counties (total area = 366,483 ha) was corn (37,840 ha) and soybean (34,200 ha) production, followed by hay (17,200 ha), winter wheat (7,970 ha), and oats (930 ha; Michigan Department of Agriculture 2002).

I generalized land-use, land-cover data (Michigan Center for Geographic Information 2001) using ArcView GIS v3.2 software (Environmental System Research Institute, Redlands, California, USA) and Spatial Analyst extension to define 13 cover types within the study area: agriculture (non-vegetated farmland, row crops, forage crops; 52.3% of study area); conifer (pines [*Pinus* spp.], other upland conifers; 1.5%); herbaceous openland (herbaceous vegetation with <25% woody cover; 2.9%); lowland deciduous forest (>60% composed of deciduous tree cover; 8.0%); lowland shrub (with >60% non-water cover; 9.9%); mixed wetland (floating aquatic vegetation, emergent wetland, mixed non-forest wetland; 3.1%); northern hardwood (>60% canopy cover of maple, beech, ash [*Fraxinus* spp.], cherry [*Prunus* spp.], birch [*Betula* spp.]; 2.3%); oak association (>60% canopy cover of oak; 1.6%); upland deciduous forest (>60% canopy cover of upland deciduous trees; 11.6%); upland shrub (>25% woody cover; <0.1%); urban (low and high intensity, roads, parks, golf courses; 2.8%); water (surface, flowing; 3.9%); and other (aspen [*Populus* spp.] association, orchards, bare ground; 0.1%). Patch size of cover types ranged from <1 ha to >11,000 ha (e.g., an agricultural matrix) and had a mean size of 29.2 ha. Consequently, generalization of spatial data may have excluded certain fine-scale landscape characteristics (e.g., hedgerows, roads) in some instances.

METHODS

Capturing Deer

I trapped deer during winter (Dec–Mar) 2004–2006, using single-door collapsible live traps (Clover 1954). Traps were placed near areas of deer activity, baited with kernel corn, and checked twice/day to minimize stress and injury to deer. My technicians and I restrained captured deer using the collapsed trap and the body weight of 1 person (Sparrowe and Springer 1970). All trapped deer were blindfolded to reduce stress and fitted with metal ear tags bearing a unique identification number (Style 681; National Band and Tag, Newport, Kentucky, USA). Individuals were aged as fawn (<1 year old), yearling (≥ 1–<2 year old,), or adult (≥ 2 years old) through general morphometric differences (e.g., shape and size of head, body size) and dental characteristics (Severinghaus 1949); ages of necropsied individuals later confirmed accuracy of field observations.

Only female deer were fitted with mortality-sensing collar-style radio-transmitters, either with VHF (Model 500; Telonics, Inc., Mesa, Arizona, USA) or VHF-GPS (Model G2000; Advanced Telemetry Systems, Isanti, Minnesota, USA) capabilities. I did not radiomark male deer because I expected low capture success for adult males based on previous trapping experience and deer behavior. Additionally, winter-captured male deer were not radiomarked because of potential problems associated with their physiological changes (i.e., neck-swelling) during the breeding season and fitting a radio-transmitter to accommodate these changes. Radio-transmitters had a unique frequency within the 150-MHz range, a mass of 270 g (VHF) or 1,100 g (VHF-GPS), and an expected minimum battery life of 36 months (VHF) or 12 months (VHF-GPS). Michigan State University's All-University Committee on Animal Use and Care approved all capturing and handling procedures for my study (Application No. 01/04-006-00).

Estimating Locations

I located deer 2–5 times/week using triangulation methods associated with telemetry (White and Garrott 1990:79–112) or from visual observations of known individuals. To increase the potential of my analyses to accurately describe space use, deer were located using a systematic sampling approach at varying time schedules on a diel basis, with ≥ 1 nocturnal location/deer/week except during capture periods. I used this sampling design because some wildlife species (including deer) potentially move at any time during a 24-hour period, and "management recommendations developed from habitat use data collected from only a portion of a 24-hour period may be ineffective" (Beyer and Haufler 1992:180). Bearings were estimated using a 3-element folding Yagi antenna (Advanced Telemetry Systems, Incorporated, Isanti, Minnesota, USA), portable radio receiver (Model R-1000, Communications Specialists, Incorporated, Orange, California, USA), and mirror-sighting compass. A global positioning system (GPS) handheld unit (Model GPS IV; GARMIN International, Incorporated, Olathe, Kansas, USA) was used to approximate the locations from which signals were received.

Locations from triangulated data were estimated using the program LOCATE III (Pacer, Truro, Nova Scotia, Canada). I used the maximum likelihood estimator (Lenth 1981*a*, *b*), as recommended by White and Garrott (1990) and Nams and Boutin (1991). Bearing standard deviation and error ellipses were estimated using LOCATE III for each location during analysis. To assess the precision of location estimates, I considered the relationship between mean error-ellipse size and landscape-patch size (Nams 1989). Given the patchiness of the study area, I assumed that characteristics of each cover type (e.g., differences in foliage densities) did not influence telemetry accuracy, resulting in my acceptance of location estimates near cover-type boundaries as accurate even if error ellipses covered ≥ 1 cover type (White and Garrott 1990:200). I used only location data from VHF signals to avoid potential differences associated with location precision between VHF- and GPS-derived location estimates (i.e., I used only VHF-derived data from VHF-GPS transmitters; see Appendix A).

Assessment of Space Use

Because habitat quality and species density are not positively correlated in some instances (e.g., social dominance factors; Van Horne 1983), my space-use analyses were estimated only for adults; i.e., I assumed that habitat quality would be higher for adults than for juveniles because deer often behave according to a social dominance hierarchy (Hirth 1977, Marchinton and Hirth 1984). Deer captured as fawns or yearlings were reclassified as adults on either the first or the second 1 June following their capture, respectively, and subsequently were used for analyses. I assumed that all location estimates that were classified in the cover type water were inaccurate and I relocated each to the nearest alternative cover type. Space use was determined seasonally based on agricultural crop production (i.e., the growing season on study area [10 May–7 Oct; 150 d], and the non-growing season [8 Oct–9 May; 215 d]). I used SYSTAT v11 (Systat Software, Inc., San Jose, California, USA) and ProStat v4.02 (Poly Software International, Inc., Pearl River, New York, USA) for statistical analyses, and 95% confidence limits (CLs; LCL = lower, UCL = upper) for space-use assessments. The use of confidence limits is advantageous in that an estimate of effect size and a measure of uncertainty are provided (Johnson 1999).

Space use is often estimated using 1 of the many home-range estimators currently available (e.g., minimum convex polygon, kernel methods, harmonic mean), and each may provide somewhat different results using the same data. One method in particular, the fixed kernel, seems to be the best estimator currently in use (see Kernohan et al. 2001). Two common methods of smoothing parameter selection for kernel estimation include the reference bandwidth (h_{ref}) method and least-squares cross-validation (h_{cv}) method (Kernohan et al. 2001). The h_{cv} method is currently recommended and was used for my analysis, as the h_{ref} method may overestimate home-range size (presumably more than the h_{cv} method) because of its relatively high bias (Worton 1995, Seaman et al. 1999).

Kernel home ranges may, however, misrepresent the space used by an animal through the inclusion of cover types containing no location estimates (Guthery et al. 2005); Sanderson (1966:231) noted that, "No doubt the home range can be reduced to some unknown minimum size." The inclusion of these apparently unused cover types may result in misguided habitat management strategies, or management effort being expended on low-priority habitat components. A new concept of resource selection that might express this minimum size is the quantification of usable space (Guthery 1997, Guthery et al. 2005).

Usable space has been described as, "the quantity (ha) of ideal (maximizes fitness), permanent habitat for a species of interest on an area of interest," where "permanent" habitat is best considered on an annual basis (Hiller et al. 2007). A permanent habitat situation might entail frequent management, depending on rates of vegetation succession in a given area. Usable space, in a qualitative sense, has been described for deer as, "the portion of a landscape that is or can be utilized by white-tailed deer, but not all space within a landscape is useful as habitat" (Fulbright and Ortega-S 2006:28). To date, known analyses formalizing the concept of usable space have been limited to use-availability data for northern bobwhites (*Colinus virginianus*) in Texas and Arkansas (Guthery et al. 2005, Hiller et al. 2007), but the concept should be valid for any wildlife species (e.g., white-tailed deer), given appropriate use-availability data. Quantifying usable space from use-availability data results in assessment of the contributions of selected cover types and the contributions of cover types randomly used and avoided.

For usable space analyses, I followed study design 3 (estimating use and availability for each individual) of Thomas and Taylor (1990) as recommended and discussed by Hiller et al. (2007). In essence, use is defined through the proportion of location estimates in a given cover type within a kernel home range, and availability as the proportional area of the given cover type within a kernel home range. Under design 3, there is no assumption of identical resource availability among individuals, and variance estimates of cover-type availability can be obtained; the use of study designs 1 or 2 could provide different results from design 3. Following Guthery et al. (2005), I based my usable space analysis on the fixed-kernel home-range estimator (Worton 1989). Usable space (U) is defined by

$$U = \sum_{i=1}^{w} u_i A_i, \tag{1}$$

where w = the number of cover types available (i = 1, 2, 3, ..., w), u_i = the unknown proportion of space that is usable in cover type i, and A_i = the area (ha) of cover type i (Guthery et al. 2005).

To solve for U, an assumption of $u_m = 1$ (i.e., the proportion of space that is usable in cover type m in a set of selected types or for data pooled over selected types equals 1) was made through support from field data (e.g., highly selected cover types based on selection indices; Hiller et al. 2007). When estimating proportions of usable space within all available cover types, assuming 1 of the cover types selected by a species as containing fully usable space makes the appropriate comparisons of usable space estimates of other cover types possible. Under this assumption, usable space within cover type i (u_i) is estimated as

$$u_i = (A_m p_i)/(A_i p_m), \tag{2}$$

where A_m = the area of cover type m, p_i = proportional use of cover type i (number of location estimates in i/total number of location estimates), and p_m = proportional use of cover type m.

The decisions related to defining cover type u_m are at the experimental unit (i.e., for each individual). If a strong selection pattern, based on selection indices, is present for 1 or 2 cover types, then these cover types will dominate usable space analyses as u_m. However, other cover types with higher selection indices and high proportions of use and availability may be substituted on an individual basis. The decision of the appropriate cover type used to describe u_m can also be supported through our knowledge of the biology of a species (i.e., cover types known to be crucial or most beneficial to a species of interest on an area of interest). To illustrate, it would be logical to assume that permanent emergent vegetation would be much more appropriate to describe cover type u_m for muskrats (*Ondatra zibethicus*) than would open water that lacks vegetation (Allen and Hoffman 1984).

I tested the relationship between the amount of usable space (y) and kernel home range size (x) using least-squares linear regression. Under this space-use relationship, when $x = 0$, y must $= 0$; i.e., a home range must contain space for the existence of usable space, so zero-intercept single-variable models were appropriate (see Guthery and Bingham 2007). I used the Pearson product-moment correlation coefficient (r) to quantify relationships between usable space and kernel home ranges.

Cover Conversion Estimation

To quantify the direction and magnitude of change (C_i) of each cover type (i) to describe fully usable space within a home range, I followed Hiller et al. (2007):

$$C_i = A(c_i - a_i), \tag{3}$$

where A = the area (ha) of interest, c_i = the proportional availability of cover type i in usable space, and a_i = the proportional availability of cover type i on the area of interest. Logically, to increase the amount of usable space by, for example, 50% (i.e., to potentially increase the abundance of a species of interest on an area of interest to some extent less than maximal), I would modify equation 3 to include the desired amount of change:

$$C_i = 0.5A(c_i - a_i), \tag{4}$$

where the coefficient of 0.5 in my example estimates a 50% increase in usable space (for cover type i). Further, I could modify equation 3 to decrease the amount of usable space for a species of interest on an area of interest (i.e., to theoretically decrease population abundance of that species). To illustrate, suppose a manager desired a substantial (perhaps 50%) decrease in the number of white-tailed deer on a management area due to concerns with agricultural crop damage. The appropriate equation would be modified to include the magnitude (e.g., 50%) and direction (e.g., −) of the desired change (decrease) in the amount of usable space. Following my example, this would be expressed by

$$C_i = -0.5A(c_i - a_i), \tag{5}$$

where the mathematical operator is reversed (i.e., from + to −) within the equation to reflect the manager's objectives (i.e., to decrease the amount of usable space). Equations can be modified similarly to reflect the specific objectives of direction and magnitude of change of usable space (or specific cover types). Note that, in my example, 0.5 does not need to be constant among cover type is; i.e., a multitude of coefficients could achieve a 50% decrease in usable space, not simply the value of 0.5 constant across all cover types within the area of interest. However, to illustrate my example, using a constant is much more intuitive to the reader.

The total amount of cover conversion (C) on the area of interest can be estimated by

$$C = \frac{\sum_{i=1}^{w} |C_i|}{2}, \tag{6}$$

the sum of the absolute values of C_i (for all $i = 1, 2, ..., w$) divided by 2. This division operation will account for the conversion of 1 cover type into another cover type (i.e., the spatial replacement of cover types).

RESULTS

Capture and Estimation of Locations

I captured and radiomarked 42 female deer. A subset of 20 radiomarked deer that were either aged as adult during capture or that moved into the adult age class during the study was available for analysis (i.e., individuals with ≥30 locations; Seaman et al. 1999). This subset contained a total of 3,493 location estimates and a mean of 71 locations/seasonal home range. I pooled data by season but not by year due to small sample sizes. The growing seasons of 2004, 2005, and 2006 included 7, 14, and 3 deer, respectively. The non-growing seasons of 2004, 2005, and 2006 included 7, 11, and 7 deer respectively. Five deer were included in similar seasonal categories for >1 year.

I pooled location estimates (3,493) from all adult deer ($n = 20$) from my study to estimate overall telemetry error. I considered telemetry error acceptable, and thus, location estimates to have acceptable precision, given the landscape characteristics of the study area (e.g., $\bar{x} = 29.2$ ha/patch), the mean telemetry error-ellipse size (10.2 ha), and the number of location estimates ($\bar{x} = 71$/deer/seasonal home range). This conclusion was based on the relationship between telemetry error and patch size (diameter ratio = 0.59) to determine appropriate sample sizes as described by Nams (1989).

The frequency distribution of all location estimates showed somewhat uneven sampling effort by month (Fig. 4.1). Effort decreased during months of deer capture (i.e., Jan, Feb, Dec, for winter; May for capture of neonates [see Chapter 2]). Sampling effort by time of day was variable and peaked during mid-day (Fig. 4.2); however, when I pooled location estimates by diel categories (diurnal = 800–1700 hr, nocturnal = remaining hours), proportional use (i.e., number of location for each cover type/total number of locations) for all cover types was similar within time periods (i.e., varied ≤ 0.06) except for agricultural areas (diurnal = 0.24, nocturnal = 0.14).

Assessment of Space Use

Kernel Home Range.—Mean kernel home-range sizes for adult female deer during the growing season ($\bar{x}$ = 77.5 ha ± 9.6 SE; n = 20) was about half that of the non-growing season ($\bar{x}$ = 140.4 ha ± 23.4 SE; n = 19), although 95% confidence intervals overlapped slightly (57.5–97.6 ha versus 91.6–189.2 ha). The mean number of cover types within home ranges was similar between seasons (6.5 ± 0.4 SE for growing, 7.4 ± 0.4 SE for non-growing). Kernel home ranges were dominated by upland deciduous forests during both seasons, while the amount of agricultural areas in kernel home ranges increased almost 2.5× from the growing to the non-growing season (Table 4.1). No cover types were used exclusively in 1 season.

Usable Space.—During the growing season, the mean amount of usable space within a kernel home range was 58.2 ha (SE = 6.9; 95% CL = 43.8–72.5); during the non-growing season, the mean amount of usable space was 103.0 ha (SE = 18.2; 95% CL = 65.4–140.6 ha). Both seasonal estimates of usable space were about three-fourths that of their respective kernel home-range estimates. The mean number of cover types containing location estimates within kernel home ranges (i.e., describing usable space) was similar between seasons (5.0 ± 0.2 SE for growing, 5.6 ± 0.3 SE for non-growing), but both were about 1 less than the mean number of cover types within kernel home ranges.

Generally, I used upland deciduous forests or conifers as the cover type that described fully usable space within a kernel home range during both seasons, based on selection indices (see Chapter 3). However, I occasionally substituted other cover types to describe fully usable space within kernel home ranges when these cover types had higher selection indices and high proportions of use and availability. Lowland shrub (7 occasions) or agriculture (6 occasions) dominated (~70%) these substitutions.

Relationship between Usable Space and Kernel Home Range.—My zero-intercept models showed a strong relationship between usable space (y) and kernel home-range size (x; Fig. 4.3). For the growing season (23 observations), usable space was a strong linear function ($r = 0.99$) of kernel home-range size described by $y = 0.73x$ (95% CL for x-coefficient = 0.68–0.78). For the non-growing season (25 observations; $r = 0.99$), the relationship was $y = 0.74x$ (95% CL for x-coefficient = 0.69–0.79). When I pooled all seasonal data, the relationship between usable space and kernel home-range size was $y = 0.74x$ ($r = 0.99$; 95% CL for x-coefficient = 0.70–0.78). Under all 3 scenarios, usable space was between 68% and 79% of the kernel home-range size, consistent with the mean amount (75%) of usable space within a kernel home range approximated earlier.

Cover Conversion Estimation

Maximizing Usable Space.—Under a management scenario to maximize usable space (i.e., 100%; theoretically maximizing deer abundance) on my study area, agricultural areas would require the greatest reduction in area during both seasons (Table 4.2). The cover types water, other, upland shrub, and urban contributed little or nothing to usable space for deer on my study area and theoretically could be converted to other cover types if achieving fully usable space were the only consideration (Table 4.2). Based on the comparison of proportional availability (study area and usable space; Table 4.2), upland deciduous forests and, to a lesser degree lowland shrubs and conifers, were cover types that existed in insufficient amounts to maximize deer abundance. Managers would need to convert about 41,221 ha (49.9%) of the study area to achieve fully usable space during the growing season, and about 37,812 ha (45.8%) during the non-growing season to achieve fully usable space, maximizing deer densities.

Decreasing Usable Space.—Following my example of a 50% decrease in usable space, an increase of 31 or 37% of agricultural areas, and a decrease of 100% of conifers and upland deciduous forests during both seasons (Table 4.2), could be part of 1 possible habitat management plan. Note that mathematically, the percent decrease in some instances (e.g., conifers, upland deciduous forests) would be <−100%; when this occurred, I used the amount (ha) of that cover type within the study area and rounded cover conversions up to −100%, as >100% of any given cover type cannot be removed. Increasing the amount of unused cover types (e.g., upland shrub, other) by 50% would also decrease usable space by 50%. Total cover conversions to meet these management objectives would be 18,060 ha (21.9% of study area) during the growing season, and 17,596 ha (21.3%) during the non-growing season.

DISCUSSION

"Common knowledge" of deer biology is often "enhanced by anecdotes and accumulated lore, speculative ideas or hypotheses [that] become transformed into a dogma that is extremely resistant to change" (McShea et al. 1997:1), which further complicates issues associated with effective deer management. Certainly, a plethora of space-use information has been published on white-tailed deer in the Midwest, but how do managers use this information to assist with habitat management decisions? Descriptions of deer home-range sizes and their vegetation structure and composition are useful, but literature may neglect a discussion of their direct relevance to the manipulation of current habitat conditions to change deer abundance on an area of interest. It would seem that a more comprehensive look at space-use by deer as it relates to habitat management would be useful for increasing the efficacy of deer management programs.

Considerations for habitat management include estimating the contributions of avoided and randomly used cover types (as determined by selection indices) under the assumption that an animal's presence in these cover types somehow contributes to their fitness. Additionally, quantifying cover conversions (or land-use changes, such as urbanization), which would theoretically change wildlife abundance, would seem logical to integrate into wildlife habitat management programs. Before quantifying potential cover conversions, I described and applied a seemingly more accurate method of quantifying space use (usable space) in comparison to the fixed-kernel estimator. My analyses showed that the concept of usable space collapsed kernel estimates into a potentially more accurate representation of space needs of deer on my study area, given my estimate of ~75% usable space within kernel home ranges. The mean number of cover types associated with usable space was about 1 cover type less than that for kernel home ranges. This thesis was based on the condition that the kernel (and other) methods often include cover types containing no location estimates, and therefore, potentially little or no use associated with these unused cover types. The assumption that my sampling methodology accurately represented deer behavior on my study area is a concern relevant to any space-use assessment.

My estimation of usable space revealed a pattern of cover use between seasons. Although the area of the 4 cover types (upland deciduous forest, lowland shrub, agriculture, conifer) that contributed most to usable space differed substantially by season (Table 4.1), the cumulative proportional contribution of these 4 cover types to usable space showed similarity (86% for growing, 88% for non-growing). For example, upland deciduous forest contributed 22.61 ha (39% of usable space) and 37.42 ha (36%) to usable space during the growing and non-growing seasons, respectively. Lowland shrub was estimated to contribute double the area to usable space for the non-growing season than the growing season (Table 4.1), yet contributed 20–23 % of total area regardless of season; other cover types also showed this trend. These patterns indicated reduced movements (i.e., reduced home-range size) of adult female white-tailed deer during and following parturition (Marchinton and Hirth 1984, Chapter 1), although the use of cover types based on usable space composition remained roughly constant regardless of season.

Cover Conversions

My study area was dominated by agriculture (52%), a relatively undesirable cover type for deer, at least in high proportions (>25%; see Cover Interspersion Rules), based on my usable space analyses and supported by selection indices calculated from southwestern Lower Michigan (Pusateri 2003). Woody cover types of varying successional stages provide suitable habitat for white-tailed deer across their geographic distribution (Baker 1984, Demarais et al. 2000). Logically, forest types dominated my usable space estimates, and white-tailed deer in the Midwest agricultural region "probably are affected more severely by forest loss than are whitetails in other regions of the country" (Gladfelter 1984:427); I attempted to quantify cover conversions under several hypothetical scenarios (e.g., agriculture converted to upland deciduous forest to increase deer abundance, upland deciduous forest converted to urban areas to decrease deer abundance) that may help managers with habitat manipulation strategies.

Urban areas, as expected, essentially contributed nothing to usable space for deer on my study area. The effects of urbanization on deer habitat may be inferred from my results. If cover conversions include increasing urbanization, as in many Midwestern states, the amount of usable space may be affected less if the converted area included cover types such as agriculture, herbaceous openland, lowland deciduous forest, northern hardwoods, oak association, or upland shrub; these cover types seemed to exist in excess based on my usable space analysis. Conversely, if urbanization included the conversion of cover types that seemed to be in quantities limiting deer abundance (e.g., conifer, lowland shrub, upland deciduous forest), then the amount of usable space for deer, and consequently deer abundance, may decline on that area. These potential conditions assume a positive relationship between deer abundance on a given area and the amount of usable space on that area, as described earlier. I do not assume that this positive relationship is linear, as limited evidence for other species has suggested otherwise (see Guthery et al. 2001:fig. 6). This evidence suggested that with the addition of usable space to an area containing near-minimum or near-maximum amounts of usable space, population abundance response may be much less than when adding usable space to an area with some intermediate amount of usable space.

Selection of u_m

I based my usable space analyses on the assumption that upland deciduous forests best described fully usable space, although conifers were also used to some degree, based on selection indices (see Chapter 3); i.e., I generally used 1 of these cover types as u_m, and assumed that other cover types described usable space at some fraction of either upland deciduous forests or conifers. Rarely, I considered cover types other than upland deciduous forests and conifers to describe fully usable space. Although selection indices (Ivlev 1961) showed conifers as having similar selection ratios ($I = 0.47$ for growing season, $I = 0.50$ for non-growing season) to upland deciduous forests ($I = 0.44$ for growing season, $I = 0.41$ for non-growing season; Chapter 3), I felt that upland deciduous forests were a more appropriate choice based on deer ecology (e.g., conifers may provide thermal or escape cover, but provide little or no food value; Schmitz 1991). Further, the mean Euclidean distance of all location estimates of deer to conifers was about 3.5× the mean distance to upland deciduous forests, and the relative importance (see Johnson 1980) of each changed depending on the spatial scale used (Chapter 3).

The importance of the cover types contributing the most to usable space for deer within southern Michigan has been suggested by another study. A space-use assessment in southwestern Lower Michigan by Pusateri (2003) estimated a mean annual kernel home-range size for primarily female deer (157.7 ha), similar to my non-growing season estimate (140.4 ha). Cover composition within home ranges described by Pusateri (2003) and selection indices (Ivlev 1961) included deciduous forest (47%; $I = 0.20$), evergreen (<4%; $I = 0.64$), and agriculture (39%; $I = -0.16$). The composition of my home-range estimates during the non-growing season were somewhat different (deciduous forest types = 37%, conifer = <8%, agriculture = 20%), but selection indices based on use-availability data provided by Pusateri (2003) generally suggested that an increase in deciduous forest and conifer, and a decrease in agriculture would be desirable if management objectives were to increase usable space for deer, which is consistent with my results. Although cover types were classified more broadly by Pusateri (2003), the general composition of cover between study areas was similar. Mean patch size differed (20.3 ha for southwestern Michigan, 29.2 ha for my study), however, suggesting that landscape characteristics and land-ownership patterns were different between study areas. Selection indices between these 2 study areas, however, were similar (Chapter 3).

Cover Interspersion Rules

I developed 3 rules of cover interspersion generalized from my results. These rules are broad enough to be implemented regardless of season, and assume management objectives that include increasing the amount of fully usable space to potentially increase deer abundance in an area similar to the agro-forest ecosystem of south central Lower Michigan.

1. The area of interest should include upland deciduous forests, conifers, and lowland shrub cover, based on their contributions to usable space and on selection indices.
2. If agricultural cover is present, it should be between 5% and 25% of the total land area. This range is loosely based on 95% CLs of proportions that agricultural areas contribute to usable space during the growing and non-growing seasons.
3. Upland deciduous forest cover and conifer cover should ideally be interspersed so that all points in the area are 100–200 m and 400–600 m from each cover type, respectively. These numbers are based on the mean Euclidean distance of location estimates from each

cover type (95% CL = 122.6–148.6 m for upland deciduous forests, 95% CL = 454.4–554.6 m for conifers; seasons combined). Because deer are a species of relatively high mobility, my suggestions for distances likely could range much broader without significantly affecting deer abundance.

Considerations

Guthery et al. (2005) discussed 2 possible explanations for the estimation of usable space in cover types that were used less than expected by northern bobwhites. Both hypotheses seem to relate to 2 basic assumptions while evaluating habitat, which may be problematic: "researchers can discern habitat selection or preference from observations of habitat use and that such selection, perceived or real, relates to fitness and hence to population growth rate" (Garshelis 2000:111). Certainly, many factors, including spatial scale of study (e.g., varying definitions of resource use and availability), may affect how use-availability data are interpreted in selection studies (e.g., Chapter 3).

The first hypothesis of Guthery et al. (2005) described density-dependent cover use, where these "avoided" cover types served as population sinks (see Pulliam 1988) under high population levels. Under high population levels, individuals may be forced into areas containing less usable space, which may affect survival and reproduction of those individuals. When populations are at a low level, more individuals are assumed to exist in areas that maximize fitness, presumably because of less intraspecific competition. Although my study area had relatively high deer densities (~27/km^2), I believe that limiting my space-use analyses to adult female deer avoided this potential problem for several reasons.

The logic behind my use of adult female deer to assess usable space was based on several considerations. First, a potential age-related social hierarchy exists among deer (Hirth 1977), which may result in differences in space use for each age class. Second, on my study area, females >1 yr old were the most abundant sex-age class (48% does, 26% bucks, 26% fawns during pre-hunt fall 2005; B. Rudolph, MDNR, personal communication). Third, female deer are often the sex class of primary interest for managers desiring relatively large reductions in population densities through strategies such as hunter-harvest (Carpenter 2000). Finally, male and female white-tailed deer may respond differently to a specific habitat manipulation technique on a management area through different resource selection strategies and space-use requirements (Stewart et al. 2003). For example, sexual segregation of deer outside of the breeding season (approximated by the growing season) may result in females selecting areas with higher quality forage (Stewart et al. 2003), indicating that adult female deer may be the best age-sex class from which to define usable space for white-tailed deer. Considering the above evidence, I believed that my selection of adult female deer effectively described usable space on my study area (and perhaps other areas of interest).

The second explanation proposed by Guthery et al. (2005) was that bobwhites may respond more to structural as opposed to compositional elements, given their relatively wide geographic distribution (Johnsgard 1975:82). The white-tailed deer also inhabits numerous vegetation types (e.g., Rolling Plains of Texas, coniferous-hardwood forests of Michigan's Upper Peninsula) and is distributed throughout most of North and Central America (Baker 1984). Under this hypothesis, if deer responded more to structural elements, then some unknown level of interchangeability may exist among cover types, and perhaps population responses to changes in the amount of usable space on a given area may not be as pronounced. To illustrate, Short (1986) considered escape cover in the southeastern coastal plains to simply be vegetation structure of a certain size and density regardless of vegetation species composition. Of course, the only way to test this hypothesis would be a long-term field study that monitors deer population dynamics, habitat manipulations, and land-use changes, which are often extraordinarily difficult (Garshelis 2000).

Temporal considerations should also be addressed when assessing usable space for any species. Although habitat conditions are not permanent, for the quantification of usable space I assumed habitat conditions to be relatively constant during the agricultural growing and non-growing seasons, and among seasons during a relatively short time period (e.g., 3 yr). Studies over longer time periods or on areas experiencing rapid land-use conversions should incorporate a study design to minimize these effects (e.g., accounting for successional changes in composition and structure for the existing habitat types).

I attempted to sample for location estimates of deer on an appropriate temporal scale relative to deer behavior (i.e., time of year, time of day; see assumption 6 of Guthery et al. 2005:661). Sampling effort was higher during 0800–1700 hr (diurnal), but general patterns of proportional use between diurnal and nocturnal time periods were similar. However, agricultural areas received more proportional use (number of location in agricultural areas/number of total locations) during diurnal hours (0.24 versus 0.14). There is evidence that deer use more open areas (e.g., agricultural fields) during the night (Montgomery 1963), and this difference in use could have potentially affected the estimated contribution of this cover type to usable space on my study area. Given the small difference in use, I felt this potential bias only minimally affected the magnitude of change of cover conversions, certainly not the direction.

I addressed some of the assumptions described by Guthery et al. (2005), as violation of ≥ 1 assumption may render my usable space estimates inaccurate to some unknown degree. Further, Guthery et al. (2005:662) stated that this "metric should be regarded as a first-generation approach," suggesting that improvements of estimating usable space may be forthcoming. Certainly, the concept of usable space should be scrutinized further by wildlife scientists for potential improvements. Here, I applied the concept of usable space to describe the space use of a species with a much different life history than northern bobwhites, the only other species known to be considered thus far. Further, I believe that my results are applicable to describe the management implications of cover-type conversions, dependent on management objectives (e.g., decreasing or increasing deer abundance) and land-use changes. My results are based on direct evidence of cover use by deer (assuming location estimates accurately represented deer behavior), which seems to be a more accurate description of space use as compared to home-range estimators such as the kernel methods. With clear evidence of use (e.g., cover types containing location estimates of deer), decisions regarding habitat management should, in theory, be better supported to achieve management objectives.

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Table 4.1. Cover type composition (ha) of 95% fixed kernel home ranges and usable space of white-tailed deer ($n = 20$) pooled by agricultural growing season (23 growing [10 May–7 Oct], 25 non-growing [8 Oct–9 May]) in south central Michigan, 2004–2006.

Season	Kernel home range		Usable space[a]		Difference	
Cover type	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Growing						
Agriculture	11.23	3.21	7.88	2.67	3.36	1.40
Conifer	8.18	2.85	7.45	2.86	0.73	0.25
Herbaceous openland	0.28	0.17	0.19	0.14	0.09	0.04
Lowland deciduous forest	4.69	1.53	3.75	1.30	0.94	0.34
Lowland shrub	17.50	3.87	11.65	2.93	5.85	1.83
Mixed wetland	2.74	2.01	2.47	2.01	0.26	0.11
Northern hardwood	2.92	0.71	1.24	0.38	1.68	0.52

Table 4.1. (cont'd)

Season Cover type	Kernel home range $\bar{x}$	Kernel home range SE	Usable space $\bar{x}$	Usable space SE	Difference $\bar{x}$	Difference SE
Growing						
Oak association	1.42	0.53	0.84	0.35	0.58	0.24
Upland deciduous forest	27.12	5.72	22.61	4.99	4.51	2.14
Upland shrub	0.00		0.00		0.00	
Urban	0.12	0.08	0.07	0.07	0.05	0.05
Water	1.32	0.62	0.00		1.32	0.62
Other	0.00		0.00		0.00	
Non-growing						
Agriculture	27.77	6.79	20.63	6.23	7.14	1.93
Conifer	10.83	3.14	9.65	3.20	1.18	0.38

Table 4.1. (cont'd)

Season	Kernel home range		Usable space		Difference	
Cover type	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Non-growing						
Herbaceous openland	1.26	0.65	0.26	0.15	0.99	0.54
Lowland deciduous forest	8.47	2.10	5.17	1.52	3.29	0.88
Lowland shrub	33.50	7.58	23.71	5.82	9.80	2.88
Mixed wetland	6.05	2.88	3.24	1.79	2.81	1.24
Northern hardwood	3.86	0.91	1.76	0.49	2.10	0.66
Oak association	2.25	0.50	1.18	0.47	1.07	0.29
Upland deciduous forest	43.89	8.92	37.42	8.83	6.47	2.04
Upland shrub	0.00		0.00		0.00	
Urban	0.14	0.10	0.00		0.14	0.10

Table 4.1. (cont'd)

Season	Kernel home range		Usable space		Difference	
Cover type	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Non-growing						
Water	2.39	0.86	0.00		2.39	0.86
Other	0.00		0.00		0.00	

[a] Usable space estimation (Guthery et al. 2005, Hiller et al. 2007) was based on use-availability data (use = proportion of location estimates within each cover type, availability = proportion of area of cover type with kernel home range) under design 3 of Thomas and Taylor (1990).

Table 4.2. Estimated cover conversions to maximize usable space (i.e., fully usable) and to decrease usable space (e.g., −50%) for white-tailed deer on an 82,636-ha study area in south central Michigan, USA, 2004–2006. Estimates were based on agricultural growing season (growing = 10 May–7 Oct for 23 home ranges; non-growing = 8 Oct–9 May for 25 home ranges; $n = 20$ deer).

	Proportional availability		Quantity of Estimated Cover Conversion			
Season Cover type	Study area (a_i)	Usable space (c_i)	Fully usable (ha; C_i)	Fully usable (%)	−50%[a] (ha; C_i)	−50%[a] (%)
Growing						
Agriculture	0.523	0.136	−32,009.3	−74.1	+16,004.7	+37.0
Conifer	0.015	0.128	+9,312.6	+730.7	−1,274.5	−100.0
Herbaceous openland	0.029	0.003	−2,161.0	−88.9	+1,080.5	+44.4
Lowland deciduous forest	0.080	0.064	−1,316.4	−19.8	+658.2	+9.9
Lowland shrub	0.099	0.200	+8,387.3	+102.7	−4,193.6	−51.3
Mixed wetland	0.031	0.042	+955.7	+37.4	−477.8	−18.7
Northern hardwood	0.023	0.021	−115.4	−6.2	+57.7	+3.1

Table 4.2. (cont'd)

	Proportional availability		Quantity of Estimated Cover Conversion			
Season	Study area	Usable space	Fully usable	Fully usable	−50%	−50%
Cover type	(a_i)	(c_i)	(ha; C_i)	(%)	(ha; C_i)	(%)
Growing						
Oak association	0.015	0.014	−84.2	−6.6	+42.1	+3.3
Upland deciduous forest	0.116	0.389	+22,565.7	+235.9	−9,565.0	−100.0
Upland shrub	<0.001	0.000	−5.3	−100.0	+2.7	+50.0
Urban	0.028	0.001	−2,188.2	−95.7	+1,094.1	+47.8
Water	0.039	0.000	−3,202.7	−100.0	+1,601.3	+50.0
Other	0.002	0.000	−138.7	−100.0	+69.3	+50.0
Non-growing						
Agriculture	0.523	0.200	−26,659.4	−61.7	+13,329.7	+30.9
Conifer	0.015	0.094	+6,466.2	+507.4	−1,274.5	−100.0

Table 4.2. (cont'd)

	Proportional availability		Quantity of Estimated Cover Conversion			
Season	Study area	Usable space	Fully usable	Fully usable	−50%	−50%
Cover type	(a_i)	(c_i)	(ha; C_i)	(%)	(ha; C_i)	(%)
Non-growing						
Herbaceous openland	0.029	0.003	−2,222.5	−91.4	+1,111.2	+45.7
Lowland deciduous forest	0.080	0.050	−2,498.4	−37.6	+1,249.2	+18.8
Lowland shrub	0.099	0.230	+10,850.3	+132.8	−5,425.1	−66.4
Mixed wetland	0.031	0.031	+44.5	+1.7	−22.3	−0.9
Northern hardwood	0.023	0.017	−465.8	−24.8	+232.9	+12.4
Oak association	0.015	0.011	−331.4	−25.9	+165.7	+13.0
Upland deciduous forest	0.116	0.363	+20,450.9	+213.8	−9,565.0	−100.0
Upland shrub	<0.001	0.000	−5.3	−100.0	+2.7	+50.0
Urban	0.028	0.000	−2,287.7	−100.0	+1,143.8	+50.0

Table 4.2. (cont'd)

	Proportional availability		Quantity of Estimated Cover Conversion			
Season	Study area	Usable space	Fully usable	Fully usable	−50%	−50%
Cover type	(a_i)	(c_i)	(ha; C_i)	(%)	(ha; C_i)	(%)
Non-growing						
Water	0.039	0.000	−3,202.7	−100.0	+1,601.3	+50.0
Other	0.002	0.000	−138.7	−100.0	+69.3	+50.0

[a] Cover conversions that exceeded the amount (ha) present on the study area were changed to the latter (i.e., >100% of any given cover type cannot be converted).

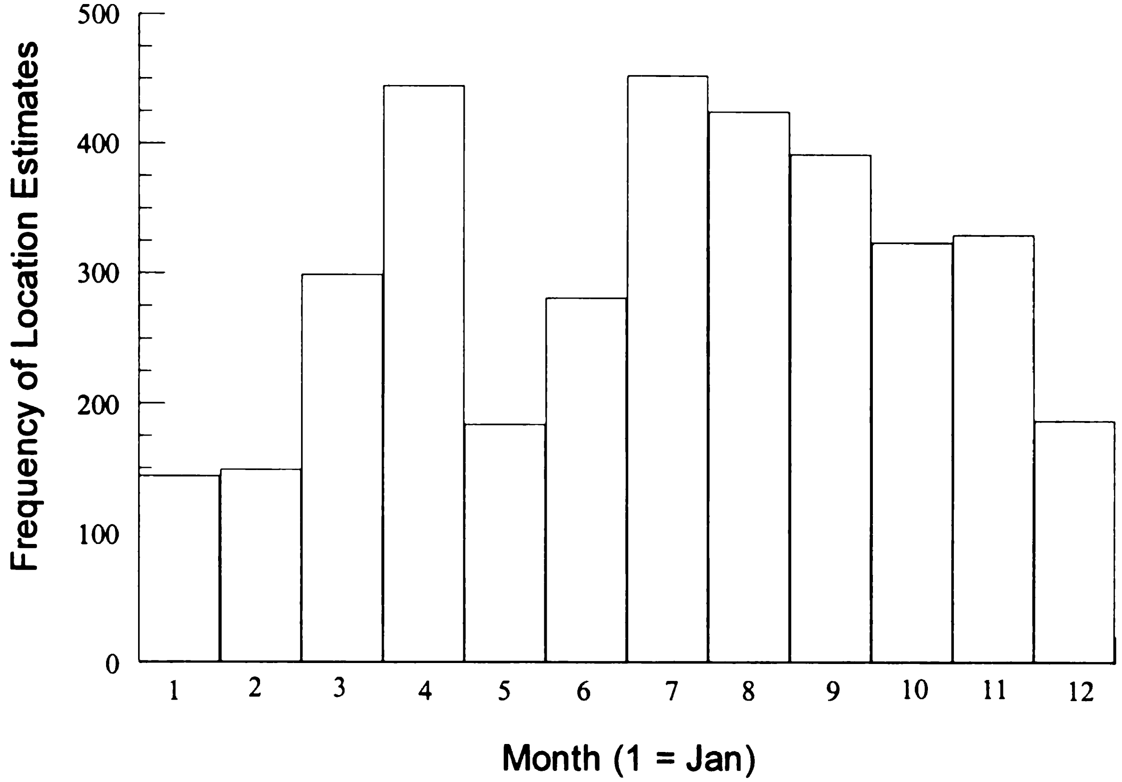

Figure 4.1. Frequency distribution of location estimates obtained through telemetry for white-tailed deer by month, south central Michigan, USA, 2004–2006.

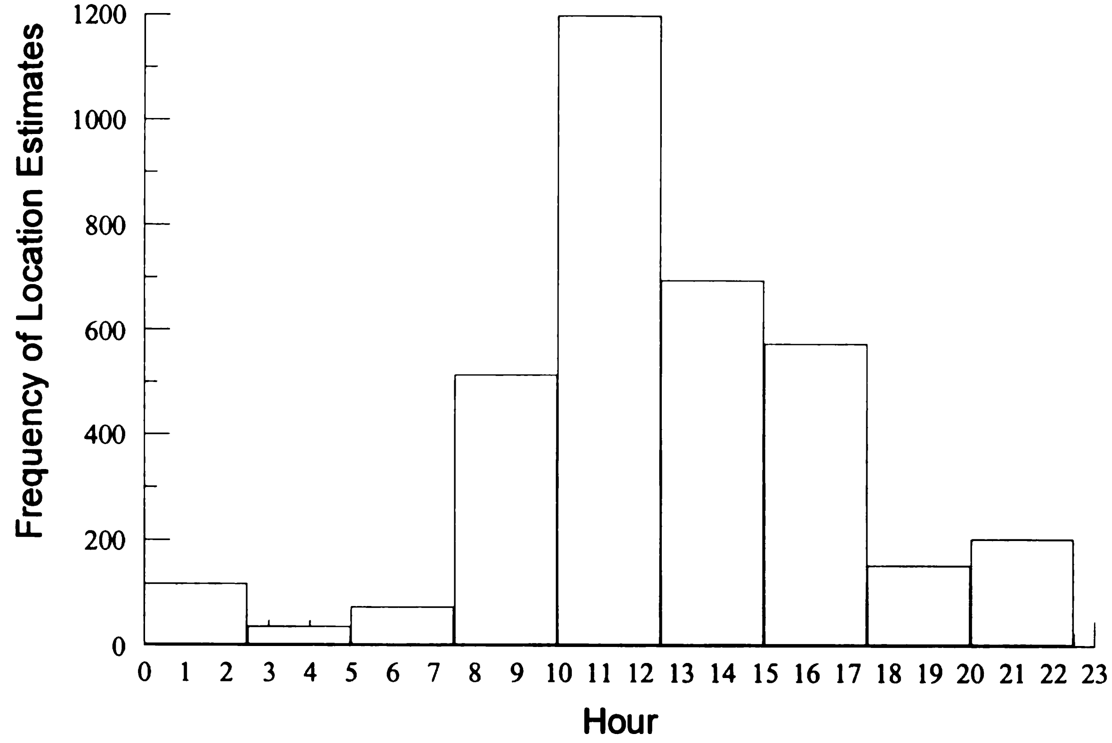

Figure 4.2. Frequency distribution of location estimates obtained through telemetry for white-tailed deer by time of day, south central Michigan, USA, 2004–2006.

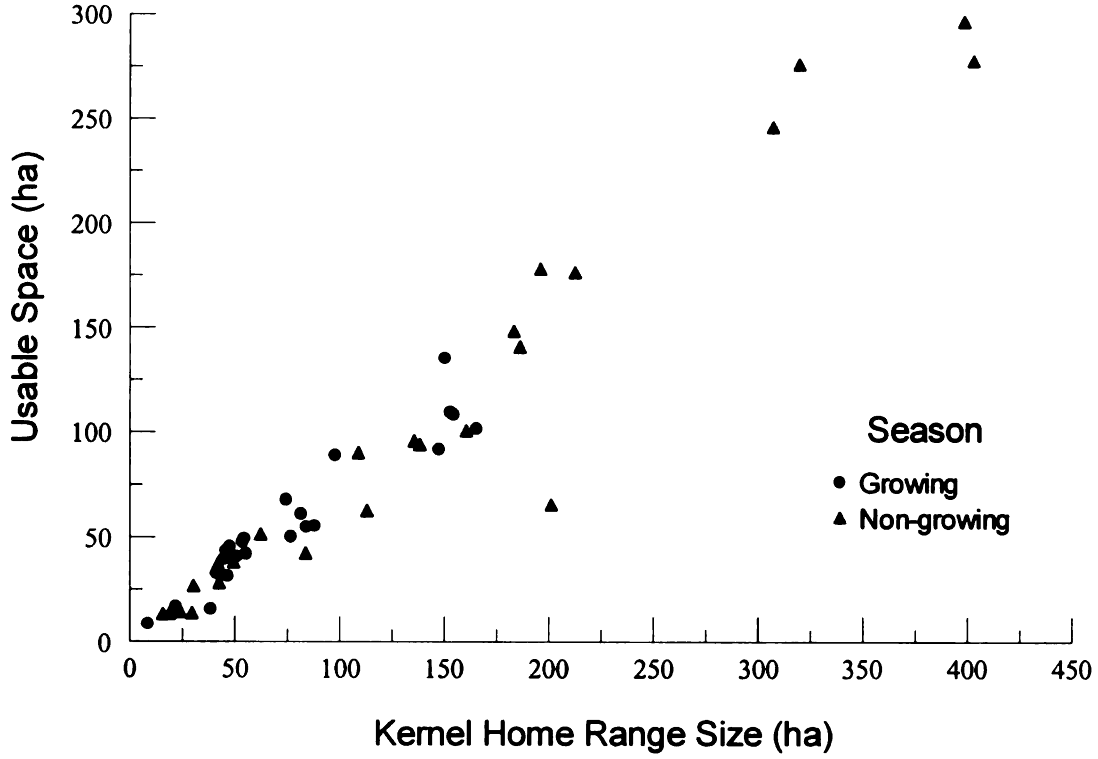

Figure 4.3. Usable space (ha) as a function of kernel home-range size (ha) by agricultural growing season (10 May–7 Oct for growing season, 8 Oct–9 May for non-growing season) for white-tailed deer in an agro-forest ecosystem, south central Michigan, USA, 2004–2006.

CHAPTER 5

Conclusions and Implications

Conclusions and Implications

Increasing deer densities, coupled with the increasing human population, will likely result in more deer-human interactions in the future. These interactions will be perceived as positive (e.g., increased hunting opportunities) or negative (e.g., increased crop damage and deer-vehicle collisions) depending on the interaction. In fact, within my study area, deer represented both positive (indicative of natural areas) and negative (deer-vehicle collisions) feelings among residents (Lischka 2006). Because deer demographics and space use varied substantially across their geographical distribution, deer population and habitat management decisions should consider science conducted locally and at multiple spatial scales because deer seem to select resources based on a selection hierarchy. However, managers should also consider regional trends to help predict the efficacy of certain strategies.

The need for proper management of deer populations also stems from their status as a game species, being the most popular big game species in North America (Smith and Coggin 1984, U.S. Fish and Wildlife Service 2001). Michigan is no exception, having about 743,000 hunters that harvested nearly 500,000 deer in 2003 (Frawley 2004). Currently, deer densities are relatively high in some areas (e.g., southern Michigan), with deer populations increasing with increases in some land-use activities (e.g., rural development, agriculture; Smith and Coggin 1984). Increases in some land-use activities and the human population further exemplify the need for effective management practices, as human-deer interactions (e.g., hunting, crop damage, deer-vehicle collisions) also increase as a result. My research attempted to characterize deer ecology in south central

Michigan in an increasingly urbanizing ecosystem to support deer-management decisions based on scientific evidence. The methods and results that I used should also have implications to deer-management issues at the regional and larger scales of management (see below) due to their uniqueness.

Population Characteristics

Knowledge of population characteristics (e.g., space use, demographics) of white-tailed deer (and other species) is directly applicable to management strategies. The efficacy of habitat management depends on accurate space-use assessments, often applied at the management-unit level, where management objectives may include increasing or decreasing deer abundance. Accurate estimates of demographics, such as age and sex structure, of a deer population are important for the accurate estimation of deer abundance (or an index of abundance) through models such as the sex-age-kill model. Harvest objectives for antlered and antlerless deer are often based on the results of such models. Without the aforementioned data, managers may unknowingly be making management decisions that do not support their objectives. For example, subject to some uncertainty, yearling female deer in this project had a higher-than-expected survival rate, and the survival rate of young fawns during their development stage and beyond was unknown in south central Michigan prior to this project. Additionally, the effects of land-ownership patterns (e.g., public vs. private) may affect deer demographics through hunter access and habitat quality, an analysis of such effects was not possible with my data given my small sample sizes.

Resource Selection

When using selection indices, large variations (e.g., large confidence intervals) are not uncommon, especially for relatively low-use and low-availability combinations of resources (Hobbs and Bowden 1982). Consequently, resource-selection ranking systems should be considered as a guide when incorporated into management decisions, not an inflexible rank of importance. When relatively strong patterns of resource selection emerge across multiple spatial scales, such as the results I presented, managers can have more confidence in their habitat-management decisions (e.g., which cover types to actively manage to improve habitat quality or quantity). Management of white-tailed deer on my study area, based on my results, would seem to be relatively consistent over multiple spatial scales. However, differences in selection may not be fully realized for multiple reasons (e.g., our lack of knowledge of deer perception), and therefore, inconsistencies should be considered depending on the spatial scale, time of year, and other factors.

At a relatively fine spatial scale (e.g., private landowners with home-range-sized units), managers may benefit from analyses done at the home-range scale to examine the life requisites of deer, and base management decisions according to their objectives. Similarly, management at the landscape scale (e.g., deer-management units within Michigan) should benefit from a coarse-scale analysis of selection to describe appropriate cover and composition of vegetation for deer. Certainly, results from a relative-importance ranking system could yield highly different ranks of resource selection across multiple spatial scales (and seasons), indicating a relatively strong selection hierarchy to consider when making management decisions. One example would seem to be the use of agricultural lands by deer on my study area. My results suggested that, at the landscape level, large patches of agriculture could theoretically limit deer population growth, but that small patches (or the edges of large patches) may be selected for foraging by deer.

Space Use

Generally, my results supported the assertion that space use varies by age class of deer; the question perhaps was the magnitude of difference more so than whether a difference existed. I provided a description of space use that included multiple age classes, but I also provided the next step by describing potential cover conversions (specific to adult female deer) that theoretically would affect deer abundance on the study area. The new concept of usable space would seem to be an appropriate, although somewhat untested, method to quantify space use and cover conversions useful for making habitat-management decisions.

A multitude of combinations exist that would theoretically decrease usable space by a desired amount. For example, removing all coniferous cover types on a given area would eliminate all usable space for deer, which theoretically could greatly reduce deer abundance on that area. This extreme scenario may not be as improbable as one might think, as areas originally covered by longleaf pine (*Pinus palustris*) forests in the southeastern U.S. have decreased by 98% (Noss et al. 1995). My study area was composed of a very small proportion of conifers (<2%), with most patches located primarily on public land. These coniferous patched do not seem to be actively managed, so succession may cause their proportion to only decrease through time. However, this illustrates the flexibility of cover conversions and should prove advantageous to managers with objectives to decrease or redistribute the densities of species on a management area, as many cover conversion limitations exist (e.g., social and edaphic factors). Certainly, managers should also consider the ecological consequences of any habitat management decision. Managers desiring a relatively high increase in high-quality habitat, however, will have to address many challenges (e.g., social, financial, and ecological constraints), and likely will not achieve the theoretical maximum amount of usable space (i.e., maximizing wildlife abundance) on their management area. The methods and information I have provided are a useful framework to follow to potentially change the relative abundance of white-tailed deer through habitat management and land-use change.

Certainly we must make several assumptions and have certain limitations when studying deer ecology. As I have discussed, questions of perception and social and financial constraints are but a few of these potential limitations. Despite this fact, I believe that the information that I have provided will be beneficial during the decision-making process for deer managers to meet their objectives. I also believe that the implications of the process that I used and the knowledge gained from this study of land-use patterns of white-tailed deer in an agro-forest ecosystem in south central Michigan will be beneficial to wildlife managers at the regional level, and perhaps beyond.

Addressing deer-habitat management issues through a multi-scale perspective and using a usable-space approach to quantify contributions of cover are both recent but seemingly useful concepts that also have relevance to population ecology of deer and other wildlife species. Habitat quality and quantity, for example, in theory is positively related to species abundance and demographics; resources selected by a species are dependent on resource availability (i.e., relative quality among a set of resources) and often age and sex structure within a population. Knowledge of deer behavior across scales and on an area-specific basis should provide a foundation on which to base deer-management decisions.

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APPENDIX A

Assessment of Precision between GPS- and VHF-derived Location Estimates

Assessment of Precision between GPS- and VHF-derived Location Estimates

INTRODUCTION

Very-high-frequency (VHF) radio-transmitters have been used in wildlife studies for approximately 50 years. One of the first published descriptions on transmitter design was by LeMunyan et al. (1959) for use with woodchucks (*Marmota monax*). Although the authors stated that the maximum range of this transmitter was only about 25 m, there should be little doubt of their preference for using these transmitters, as relocation of woodchucks was often "extremely difficult and frequently required a considerable amount of digging, only to discover that the burrow was empty" (LeMunyan et al. 1959:107). Radio-transmitters have not only made the wildlife researcher's job easier, but they have also helped researchers answer many questions that previously could not be answered, at least not with much certainty. Since those early days, radio-transmitters have become a mainstay in wildlife science.

Animal movements and resource selection are important aspects often studied using radiomarked individuals. Telemetry techniques are used to estimate locations of VHF-radiomarked individuals, either using homing (i.e., a visual confirmation of an animal's location) or triangulation (White and Garrott 1990). Other field data may also be collected, depending on transmitter capabilities, such as body or operative temperatures (e.g., Lonsdale et al. 1971), and heart rates (e.g., Kanwisher et al. 1978). Researchers must consider several assumptions when using marked animals, however, including that the radiomark does not affect animal behavior (White and Garrott 1990).

New technology occasionally but consistently makes its way into wildlife science. Global Positioning System (GPS) telemetry technology for wildlife studies was introduced around 1992 (Rodgers et al. 1996) and has become increasingly prevalent in wildlife science during the past 10 years, especially for studying large mammals. Although GPS-capable collars often cost $\leq 10\times$ that of conventional VHF radio-transmitters designed for similar applications, the automatically scheduled fixes obtained through GPS technology may minimize animal relocation effort after transmitter deployment.

Before 2000, selective availability (SA) degraded the precision and accuracy of GPS-derived locations. However, post-SA GPS locations are still not without error (cf. Cain et al. 2005), and fixes should still be treated as location estimates as opposed to actual locations of radiomarked individuals. Assessing the accuracy of these systems under actual field conditions has occurred (e.g., Cargnelutti et al. 2007, Sager-Fradkin et al. 2007), but a comparison of GPS-derived location estimates with simultaneous VHF-derived estimates (i.e., a measure of precision) in various wildlife habitat conditions seems lacking.

My objective was to assess location precision between GPS- and VHF-derived location estimates in an agro-forest landscape in southern Lower Michigan. I assessed precision using 2 scenarios. For the first scenario, I used a relatively controlled field experiment by comparing GPS locations estimated using a handheld unit to VHF locations estimated using triangulation. For the second scenario, I used free-ranging white-tailed deer (*Odocoileus virginanus*) radiomarked with GPS-VHF radio-transmitters to compare automatically scheduled GPS fixes to simultaneous VHF locations estimated using triangulation under actual field conditions. I also assessed cover-type assignment consistency between GPS- and VHF-derived location estimates using a GIS.

STUDY AREA

My study took place during 2004–2006 in eastern Jackson (Grass Lake, Henrietta, and Waterloo townships) and western Washtenaw (Dexter, Lima, Lyndon, and Sylvan townships) counties in an agro-forest landscape in south central Lower Michigan. The physiographic regions of this area are Hillsdale-Lapeer Hilly Upland, South Central Rolling Plain, and Southeastern Rolling Plain (Sommers 1977:24) with alfisols as the major soil order (Sommers 1977:36). Surface formations in the study area are the result of glaciation and include all 4 types present within Michigan (moraine, till plain, outwash plain, and lacustrine plain; Sommers 1977:32). Elevation of the study area ranged approximately 180–300 m and consisted of relatively limited relief (Sommers 1977:26, 33).

METHODS

I used the distance between GPS-estimated locations and VHF-estimated locations to assess location precision. All statistical analyses were performed using SYSTAT v11 (Systat Software, Inc., San Jose, California, USA) and ProStat v4.02 (Poly Software International, Inc., Pearl River, New York, USA) software. I made comparisons using 95% confidence limits (CLs; LCL = lower, UCL = upper) and *t*-tests, and used linear regression to assess the relationship between time to triangulate VHF-location estimates and time to complete triangulations. To test for a systematic bias in direction between GPS and VHF location estimates, I arbitrarily used GPS locations as the origin on a coordinate system and plotted VHF location estimates in relation to this origin. Circular statistics were used to determine mean angle if VHF location estimates were not uniformly distributed using the Rayleigh test for randomness (Batschelet 1981) at $\alpha = 0.05$.

Stationary VHF Transmitters

During 8 time periods throughout the study, I placed 6 transmitters (either 3 each of 2 models or 6 of 1 model) of VHF radio-transmitters in various cover types. Both radio-transmitters were suitable for white-tailed deer, 1 for neonates (Model M4210; Advanced Telemetry Systems, Isanti, Minnesota, USA), and 1 generally for deer ≥ 6 months old (Model 500; Telonics, Inc., Mesa, Arizona, USA) or similar-sized wildlife species. I attempted to place radio-transmitters in a relatively systematic manner in various cover types throughout the study area (e.g., agricultural areas, upland deciduous forests, lowland shrubs), during several seasons, and at various distances from roadways in an attempt to simulate actual field conditions. Transmitter locations were estimated using a handheld GPS unit (Model GPS IV; GARMIN International, Incorporated, Olathe, Kansas, USA).

Animal-borne GPS-VHF Transmitters

I captured deer during winter (Dec–Mar) 2004–2006, using single-door collapsible live traps (Clover 1954). Traps were placed near areas of deer activity, baited with kernel corn, and checked twice daily to minimize stress and injury to deer. My technicians and I restrained captured deer using the collapsed trap and the body weight of 1 person (Sparrowe and Springer 1970). All trapped deer were blindfolded to reduce stress and fitted with metal ear tags bearing a unique identification number (Style 681; National Band and Tag, Newport, Kentucky, USA). Only adult female deer were fitted with mortality-sensing collar-style GPS-VHF radio-transmitters (Model G2000; Advanced Telemetry Systems, Isanti, Minnesota, USA) due to transmitter weight (1,100 g). Radio-transmitters had a unique frequency within the 150-MHz range and an expected minimum battery life of 12 months. I scheduled GPS-fix intervals for 1 fix every 9 hours (Jan-Nov) or 3 hours (Nov–Dec), and remotely released transmitters from deer approximately 11 months post-deployment. Michigan State University's All-University Committee on Animal Use and Care approved all capturing and handling procedures for my study (Application No. 01/04-006-00).

Triangulations

Observers located stationary VHF radio-transmitters and GPS-VHF-marked deer using triangulation methods. Each of 6 observers was given transmitter frequencies and a vague general description of where each transmitter signal could be received. Transmitters used were based on availability at the time of each trial. Azimuths were estimated using a 3-element folding Yagi antenna (Advanced Telemetry Systems, Incorporated, Isanti, Minnesota, USA), portable radio receiver (Model R-1000, Communications Specialists, Incorporated, Orange, California, USA), and mirror-sighting compass. A handheld GPS unit was used to approximate the locations from which signals were received. Observers also recorded date and time to complete each triangulation. After triangulations of stationary VHF transmitters were completed, observers recovered transmitters from the field. Locations from triangulated data were estimated using the program LOCATE III (Pacer, Truro, Nova Scotia, Canada). I used the maximum likelihood estimator (Lenth 1981*a*, *b*), as recommended by White and

Garrott (1990) and Nams and Boutin (1991). Ninety-five percent error ellipses were estimated using LOCATE III for each location during analysis.

Cover-type Classification

I generalized land-use, land-cover data (Michigan Center for Geographic Information 2001) using ArcView GIS v3.2 software (Environmental System Research Institute, Redlands, California, USA) and Spatial Analyst extension to define 13 cover types within the study area: agriculture (non-vegetated farmland, row crops, forage crops; 52.3% of study area); conifer (pines [*Pinus* spp.], other upland conifers; 1.5%); herbaceous openland (herbaceous vegetation with <25% woody cover; 2.9%); lowland deciduous forest (>60% composed of deciduous tree cover; 8.0%); lowland shrub (with >60% non-water cover; 9.9%); mixed wetland (floating aquatic vegetation, emergent wetland, mixed non-forest wetland; 3.1%); northern hardwood (>60% canopy cover of maple, beech, ash [*Fraxinus* spp.], cherry [*Prunus* spp.], birch [*Betula* spp.]; 2.3%); oak association (>60% canopy cover of oak; 1.6%); upland deciduous forest (>60% canopy cover of upland deciduous trees; 11.6%); upland shrub (>25% woody cover; <0.1%); urban (low and high intensity, roads, parks, golf courses; 2.8%); water (surface, flowing; 3.9%); and other (aspen [*Populus* spp.] association, orchards, bare ground; 0.1%). Patch size of cover types ranged from <1 ha to >11,000 ha (e.g., an agricultural matrix) and had a mean size of 29.2 ha.

I used a general vegetation canopy description of either open (agricultural areas and grasslands) or closed (forest and shrub cover types) at the site of each stationary transmitter to test for effects of vegetation on location precision. I also used the GIS cover-type classification system to test for differences in cover-type assignment between VHF and GPS location estimates for both stationary and animal-borne transmitters.

RESULTS

Stationary VHF Transmitters

For stationary transmitters, I found no differences among observers (*n* = 6 observers for 64 VHF location estimates) based on 95% CLs of distances between VHF location estimates (triangulation) and GPS estimates of radio-transmitters (handheld GPS unit). Observers completed each triangulation in 14.3 min (SE = 0.8) on average, and were positioned an average distance of 465.3 m (SE = 18.7) from transmitters when azimuths (*n* = 192) were estimated. I also found no transmitter model (95% CL = 113.1–217.2 for neonate, *n* = 21; 95% CL = 136.2–178.0 for adult, *n* = 43) or season effects (95% CL = 130.9–184.3 for spring, *n* = 24; 95% CL = 129.8–198.9 for summer, *n* = 34; 95% CL = 50.4–233.9 for winter, *n* = 6). Error ellipses based on triangulations averaged 9.5 ha (SE = 2.0) and the distribution of error ellipse size was skewed right (Fig. A.1). Locations estimated by the handheld GPS unit were contained within 38% of VHF error ellipses.

The mean overall distance between VHF location estimates and GPS estimates was 159.7 m (SE = 10.6, 95% CL = 138.5–181.0). When I plotted distance as a function of the time needed to complete triangulation (Fig. A.2), no relationship existed. Using the Rayleigh test, I found the angles between GPS and VHF location estimates to be uniformly distributed ($P \approx 0.8$; Fig. A.3), indicating no systematic directional error between GPS- and VHF-derived estimates.

Using my canopy classification system, closed (95% CL = 122.7–179.3, *n* = 40) and open (95% CL = 141.0–207.6, *n* = 24) canopy coverage did not seem to affect precision between VHF and GPS location estimates. Cover-type assignments between GPS- and VHF-derived locations were consistent 86% (55 of 64 instances) of the time. One GPS-derived location was incorrectly assigned (water) using my GIS cover classification system, which was likely due to error caused by generalization of spatial data.

Animal-borne GPS-VHF Transmitters

I captured 42 female deer, of which 4 adults were marked with GPS-VHF radio-transmitters. The GPS-VHF radio-transmitters (*n* = 4) recorded a total of 2,219 GPS fixes (77% were 3-dimensional) to estimate locations of deer. One GPS-VHF radio-transmitter failed to obtain any GPS fixes after <1 month of deployment due to a faulty antenna and failed to collect any simultaneous data. From the 3 GPS-VHF transmitters, observers obtained only 20 VHF triangulations of location estimates that I considered simultaneous (i.e., ± 15 min) with GPS fix times, so I pooled locations regardless of individual or year. Ninety percent of these 20 GPS fixes were 3-dimensional. Scheduled fixes from GPS-VHF radio-transmitters were routinely delayed, which greatly reduced the ability to predict and obtain simultaneous VHF triangulations. A mean of 12.6 min (SE = 0.8) was used by observers to complete VHF triangulations. Mean distance between GPS fixes from animal-borne GPS-VHF transmitters and simultaneous VHF location estimates was 304.1 m (SE = 54.5; 95% CL = 190.0–418.3). Error ellipses averaged 19.6 ha (SE = 7.4) and the frequency distribution of ellipse size was skewed right (Fig. A.4). Estimates of GPS-derived locations were contained within 30% of VHF error ellipses.

I found a weak linear relationship when the distance between triangulated location estimates and GPS fixes ($n = 20$) of animal-borne GPS-VHF radio-transmitters was plotted as a function of time needed to complete each triangulation ($y = 41.4x - 217.8$; $r = 0.62$; Fig. A.5). Angles between GPS and VHF location estimates were not distributed uniformly, however ($P = 0.04$; Fig. A.6); the mean angle between GPS and VHF estimates was 9.7°.

Of 20 GPS fixes, 13 (65%) were assigned to cover types consistently with VHF location estimates. Mean GPS-to-VHF distances between consistently and inconsistently assigned cover types were 284.6 m and 340.3 m, respectively, although 95% CLs overlapped (132.1–437.2 m for consistent assignment, 116.6–564.1 m for inconsistent assignment); based on my sample size, distance may not have been related to consistency of cover-type assignment.

DISCUSSION

My objective was to assess location precision between GPS- and VHF-transmitters, and I consider both to provide estimated, not actual, locations. Locations based on GPS fixes certainly are not free from error, and this error can be highly variable (Cargnelutti et al. 2007). Many variables can influence location precision with the GPS units, including topography, animal behavior, vegetation, and brand of unit (Cain et al. 2005, Cargnelutti et al. 2007, Hebblewhite et al. 2007), similarly to VHF radio-transmitters. Perhaps most importantly, observation-rate bias (i.e., systematically failed GPS fixes) from missing data could bias resource selection assignment more than location errors (Johnson et al. 1998, Sager-Fradkin et al. 2007). Relatively fine-scale movements of animals may be particularly difficult to ascertain from GPS-derived location error (Ganskopp and Johnson 2007). This may have contributed to the lower precision of animal-borne location estimates in comparison to stationary location estimates, as well as the greater inconsistency of cover-type assignment of animal-borne transmitters in comparison to stationary transmitters.

It is unclear whether animal movements, imprecise GPS fixes, or vegetation caused increased location error between VHF and GPS location estimates, but I had no evidence that animal-borne GPS units were free of location error or more accurate than VHF radio-transmitters; in fact, some level of systematic error may have been present among animal-borne estimates (Fig. A.6). The time ($\bar{x}$ = 12.6 min) observers needed to complete triangulations on animal-borne transmitters was similar to that needed for stationary transmitters ($\bar{x}$ = 14.3 min), but as time to complete triangulations increased, distances between GPS fixes and VHF location estimates increased (Fig. A.5). This provides some evidence that animal movements may have contributed to a lack of precision between GPS- and VHF-derived location estimates, and if time to triangulate was minimized, this type of error should be minimized. The primary advantage of GPS units, depending on study objectives and unit model, would seem to be less field effort (e.g., VHF triangulations unnecessary due to automatic GPS fixes) after deployment, and a potentially larger location data set. Other GPS advantages could include data describing temperature and altitude, and the remote release of GPS units to allow recovery when desired.

Although I found no difference in precision when considering canopy cover (open or closed) for stationary VHF transmitters, a larger sample size may provide more information about canopy effects. The use of a handheld GPS unit by an observer to estimate a location may provide different location error or bias than an animal-borne GPS-transmitter with a fix schedule. Canopy cover, especially in forested vegetation types, has been shown to strongly bias GPS location estimates, which may be dependent on sampling rates (DeCesare et al. 2005). Very-high-frequency systems are also subject to the effects of vegetation, as well as the distance between the receiver and the transmitter during triangulations (Chu et al. 1989). Researchers' decisions on which system is most appropriate for their study may be based on research objectives, financial constraints, species under study, cover types within the study area, and field effort, as each system has advantages and disadvantages.

MANAGEMENT IMPLICATIONS

Resource selection studies may be most influenced by location errors, as the animal-borne units and VHF triangulations were imprecise 35% of the time for cover-type assignment. The accuracy of assignment, however, is also important and several studies have assessed this issue. Erroneous assignment of resource use, especially due to systematic error, could impact management decisions regarding habitat management and other practices. Tests of location precision, and when possible, location accuracy should be performed for studies using radiomarked animals, regardless of whether VHF or GPS units are used. When assessing telemetry precision and accuracy, researchers should consider study and sampling designs (e.g., when and how often to sample) as well as the natural history (e.g., when and how often animals move) of the species under study.

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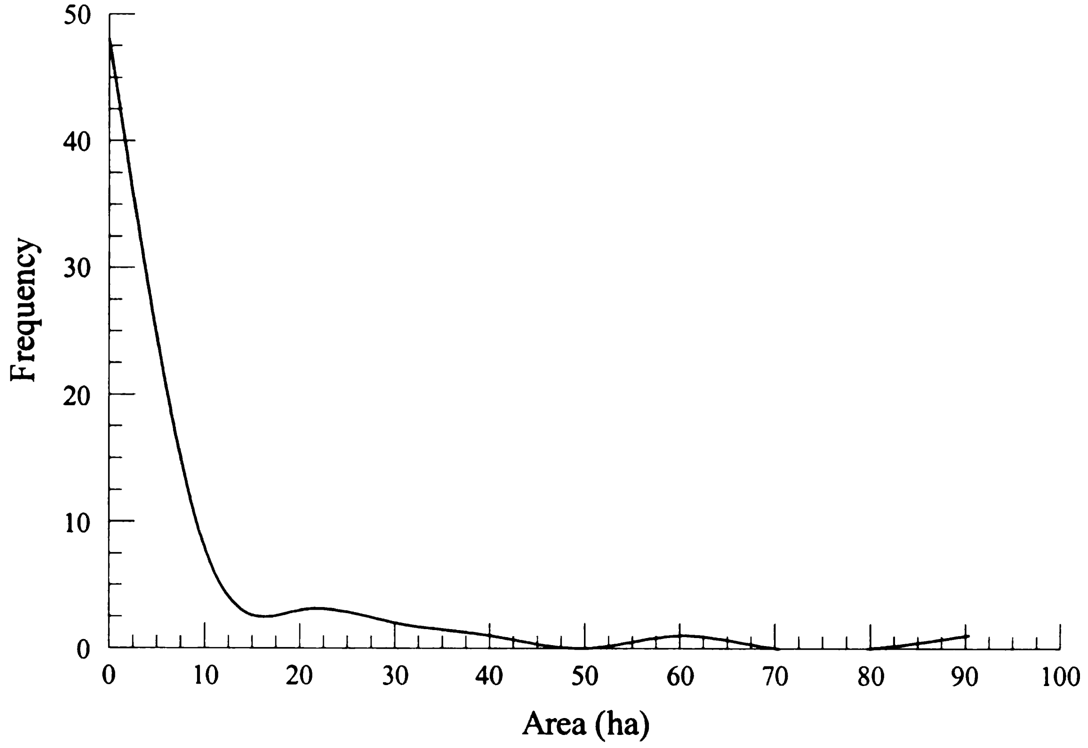

Figure A.1. Frequency distribution of error ellipses of stationary VHF radio-transmitters using triangulation to estimate 64 locations in an agro-forest landscape, south central Michigan, USA, 2004–2006.

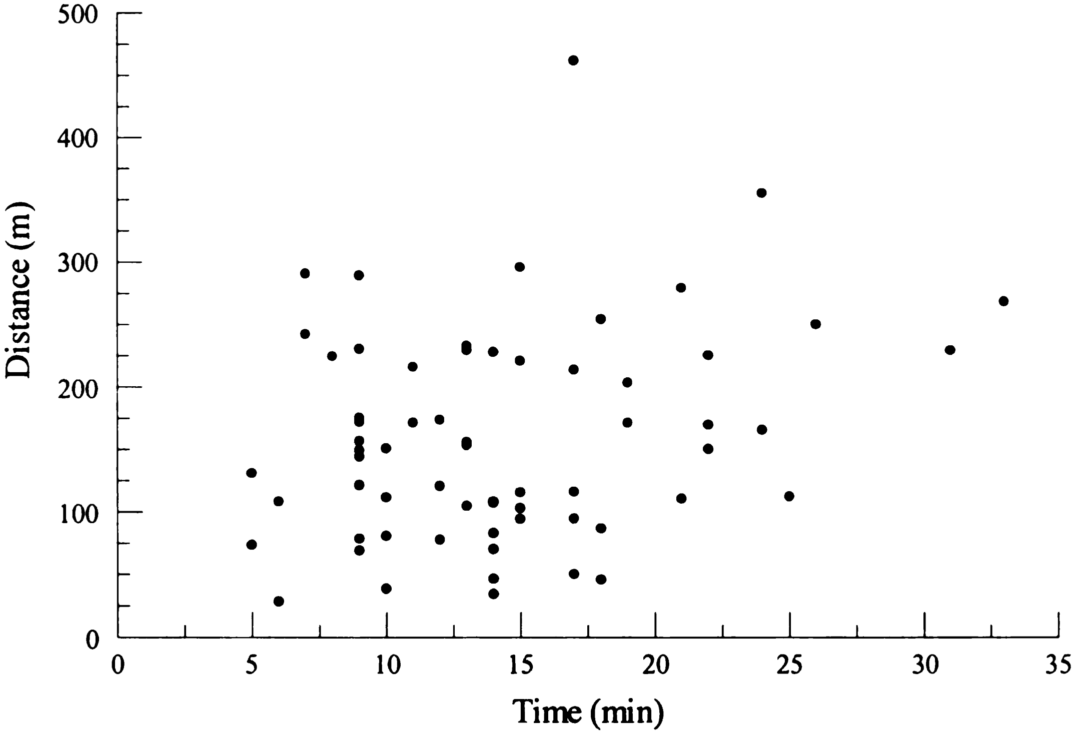

Figure A.2. Distances between triangulated VHF location estimates and GPS fixes (n = 64) from a handheld unit of stationary VHF radio-transmitters as a function of time to complete each triangulation, south central Michigan, USA, 2004–2006.

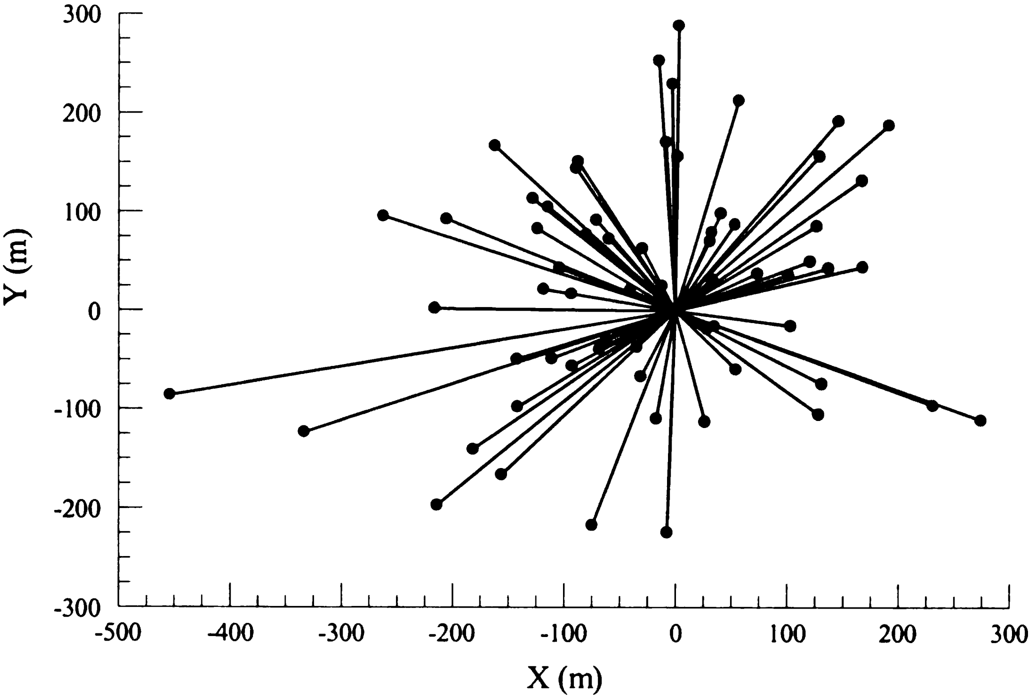

Figure A.3. Distribution of location estimates of stationary VHF radio-transmitters using triangulation and point estimates using a handheld GPS unit. Distribution reflects the relationship between 64 GPS fixes indexed with the coordinate origin and VHF location estimates.

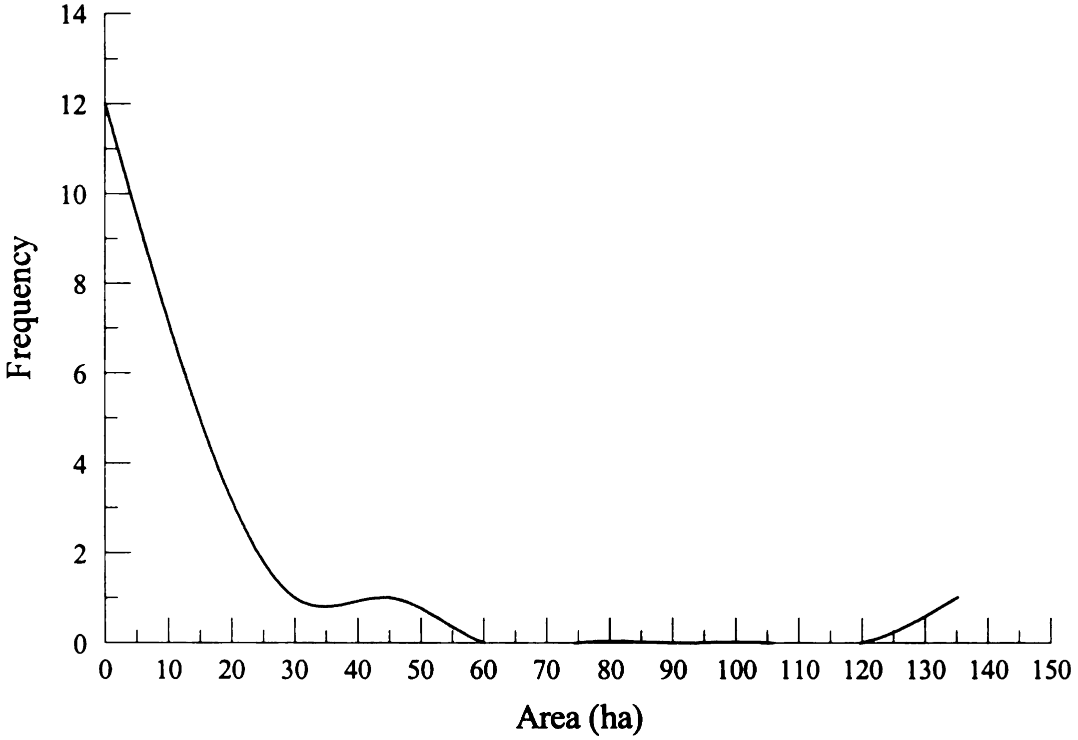

Figure A.4. Frequency distribution of error ellipses of animal-borne GPS-VHF radio-transmitters using triangulation to estimate 20 locations of white-tailed deer in an agro-forest landscape, south central Michigan, USA, 2004–2006.

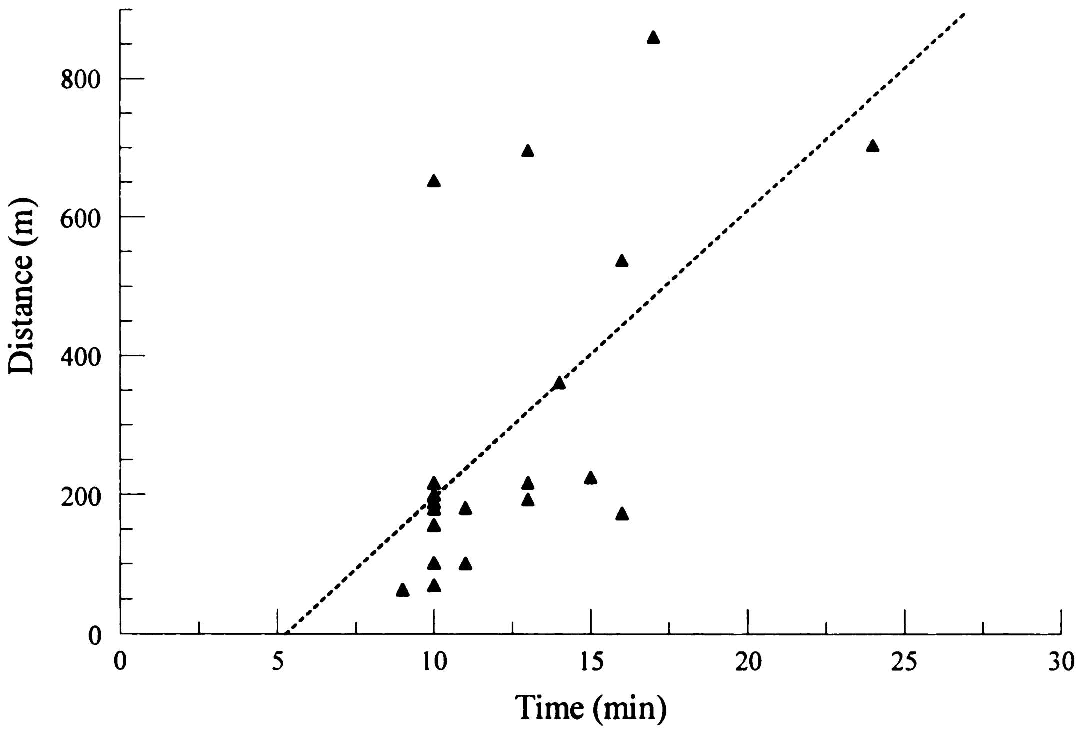

Figure A.5. Distances between triangulated location estimates and GPS fixes (n = 20) of animal-borne GPS-VHF radio-transmitters as a function of time to complete each triangulation, south central Michigan, USA, 2004–2006. Dashed line represents linear regression model ($y = 41.4x - 217.8$; $r = 0.62$) describing relationship.

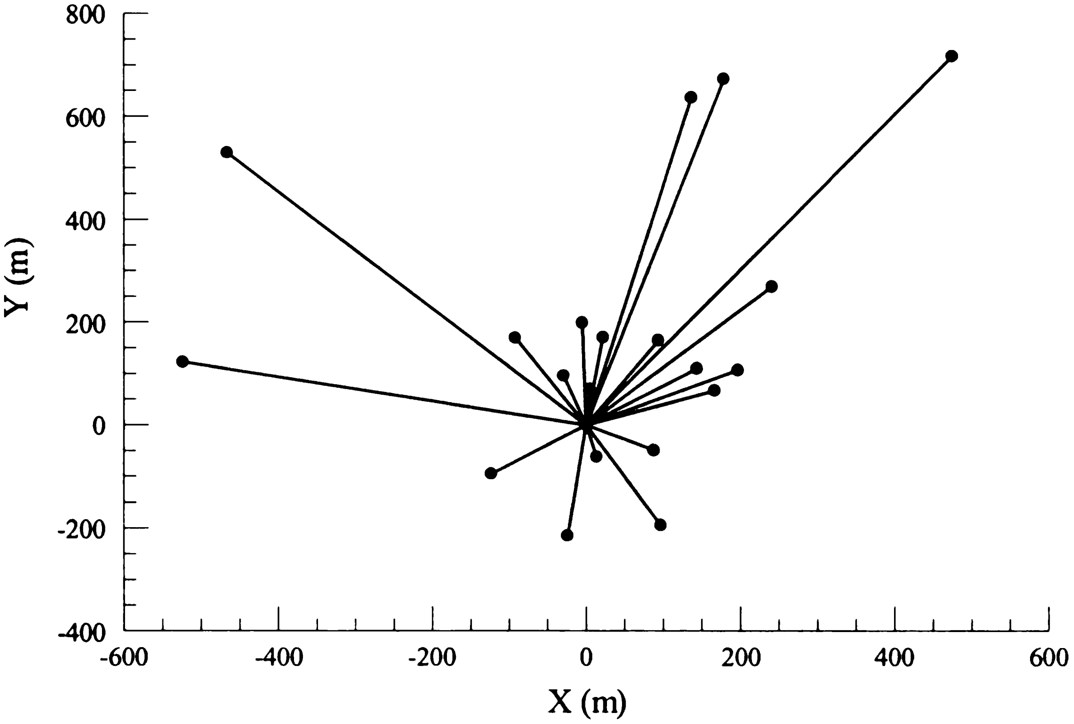

Figure A.6. Distribution of location estimates using animal-borne GPS-VHF radio-transmitters, south central Michigan, 2004–2006. Distribution reflects the relationship between 20 GPS fixes indexed with the coordinate origin and simultaneous VHF location estimates of radiomarked white-tailed deer (*n* = 3) using triangulation.

APPENDIX B

Capture and Fate Descriptions of White-tailed Deer

Table B.1. Capture and fate information of radiomarked female white-tailed deer captured using Clover traps, south central Michigan, USA, winters 2004–2006.

Tag	Date of Capture	Age Class at Capture[a]	Fate[b]
MSU 10	1/31/2005	A	capture myopathy
MSU 75	1/29/2004	Y	collar slipped
MSU 86	2/24/2004	A	hunter-harvest
MSU 87	2/6/2004	Y	hunter-harvest
MSU 88	2/16/2004	A	unknown
MSU 89	3/12/2004	Y	vehicle collision
MSU 91	2/3/2004	F	collar slipped
MSU 94	2/3/2004	Y	hunter-harvest
MSU 95	3/15/2004	A	hunter-harvest
MSU 96	2/4/2004	F	collar slipped
MSU 97	1/6/2005	Y	transmitter failure
MSU 98	3/10/2004	Y	removed GPS collar
MSU 101	1/8/2005	Y	trauma (old)
MSU 104	1/11/2005	A	hunter-harvest
MSU 105	1/12/2005	F	collar trauma
MSU 106	1/21/2005	F	trauma, malnutrition
MSU 107	1/11/2005	F	transmitter failure
MSU 109	1/25/2005	Y	alive
MSU 110	1/25/2005	F	unknown
MSU 113	1/8/2005	Y	hunter-harvest
MSU 115	1/20/2005	F	unknown
MSU 116	1/27/2005	A	collar slipped
MSU 117	1/27/2005	F	alive at end of study
MSU 120	1/27/2005	Y	hunter-harvest
MSU 122	3/3/2005	A	removed GPS collar
MSU 123	3/23/2004	A	hunter-harvest
MSU 124	1/6/2005	Y	capture myopathy
MSU 134	12/21/2004	F	collar slipped
MSU 136	1/31/2005	A	alive
MSU 138	2/24/2005	Y	hunter-harvest
MSU 139	3/2/2005	F	alive
MSU 148	2/9/2006	F	alive
MSU 159	1/20/2006	A	alive
MSU 160	3/16/2006	F	alive
MSU 162	2/11/2006	A	hunter-harvest

Table B.1. (cont'd)

Tag	Date of Capture	Age Class at Capture[a]	Fate[b]
MSU 163	2/9/2006	F	vehicle collision
MSU 166	2/28/2006	A	hunter-harvest
MSU 167	1/10/2006	F	unknown
MSU 169	2/11/2006	F	dropped break-away collar
MSU 171	2/24/2006	A	removed GPS collar
MSU 176	12/20/2004	A	hunter-harvest
MSU 178	1/8/2005	F	collar slipped
unknown	2/17/2004	F	capture myopathy

[a] F = fawn (<1 yr old), Y = yearling (≥ 1–<2 yr old), A = adult (≥ 2 yr old).

[b] Unknown included deer that may have dispersed long distances or unconfirmed transmitter failures; alive = alive at conclusion of field data collection.

Table B.2. Capture and fate information of ear-tagged male white-tailed deer captured using Clover traps, south central Michigan, USA, winters 2004–2006.

Tag	Date of Capture	Age Class at Capture[a]	Fate
MSU 80	2/11/2004	A	unknown
MSU 85	1/28/2004	F	unknown
MSU 90	2/25/2004	Y	unknown
MSU 92	1/6/2005	F	unknown
MSU 93	2/19/2004	F	unknown
MSU 99	2/2/2004	A	unknown
MSU 102	1/6/2005	F	unknown
MSU 103	1/11/2005	F	unknown
MSU 108	1/21/2005	F	unknown
MSU 111	12/20/2004	F	hunter-harvest
MSU 112	1/26/2005	F	unknown
MSU 114	1/13/2005	F	hunter-harvest
MSU 118	1/26/2005	F	hunter-harvest
MSU 125	3/24/2004	F	unknown
MSU 135	12/21/2004	F	unknown
MSU 140	3/8/2005	F	unknown
MSU 142	2/5/2005	Y	vehicle collision
MSU 144	2/2/2005	F	vehicle collision
MSU 161	1/10/2006	F	hunter-harvest
MSU 165	1/9/2006	F	unknown
MSU 168	2/24/2006	F	unknown
MSU 170	1/25/2006	F	unknown
MSU 175	3/17/2006	F	hunter-harvest
MSU 177	1/11/2005	Y	hunter-harvest

[a] F = fawn (<1 yr old), Y = yearling (≥ 1–<2 yr old), A = adult (≥ 2 yr old).

Table B.3. Capture and fate information of neonate white-tailed deer captured during May–June 2004–2006 and radiomarked with break-away radio-collars, south central Michigan, USA.

Tag	Date of Capture	Sex	Estimated Age at Capture (d)	Fate[a]
MSU 126	5/21/2004	M	8.0	canid-kill
MSU 127	5/25/2004	M	8.4	malnutrition
MSU 128	5/26/2004	M	8.4	collar dropped
MSU 129	5/27/2004	F	7.2	hunter-harvest
MSU 130	5/30/2004	F	6.9	vehicle collision
MSU 131	6/1/2004	M	6.8	unknown
MSU 132	6/4/2004	F	5.8	collar dropped
MSU 133	6/11/2004	F	10.3	collar dropped
MSU 137	5/25/2005	M	8.1	canid-kill
MSU 143	5/28/2005	F	7.4	vehicle collision
MSU 145	5/16/2005	M	7.7	canid-kill
MSU 146	5/25/2005	F	7.2	canid-kill
MSU 147	5/26/2005	F	6.6	collar dropped
MSU 149	5/31/2005	M	9.2	unknown
MSU 150	5/17/2004	M	5.5	hunter-harvest
MSU 151	5/28/2005	M	8.4	collar dropped
MSU 153	5/26/2005	M	7.0	alive
MSU 155	5/31/2005	M	8.5	canid-kill
MSU 156	5/29/2005	F	7.3	collar dropped
MSU 157	5/17/2006	M	6.3	hunter-harvest
MSU 158	5/17/2006	M	6.6	hunter-harvest
MSU 182	5/27/2006	F	8.2	collar dropped
MSU 183	5/17/2006	M	6.0	alive
MSU 184	6/2/2006	M	7.0	alive
MSU 185	5/9/2006	M	6.6	alive
MSU 186	5/17/2006	M	8.7	alive
MSU 187	5/18/2006	F	5.9	capture mortality
MSU 188	5/25/2006	F	8.2	alive
MSU 189	5/25/2006	F	6.1	alive
MSU 190	5/25/2006	F	5.7	alive
MSU 191	6/1/2006	M	7.3	alive
MSU 192	6/1/2006	M	5.5	alive
MSU 193	6/5/2006	F	4.0	vehicle collision
MSU 194	6/5/2006	F	7.5	unknown injury[b]

[a] Unknown cause of mortality due to consumption of carcass; alive = alive at conclusion of field data collection.

[b] Found injured by a wildlife rehabilitator and censored from study.