

Home Range, Habitat Use, Edge Relationships, Mortality Sources, Age Structure, and Survival of White-Tailed Deer on Mount Desert Island, Maine, 1992-1994.

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EXECUTIVE SUMMARY

Deer populations were studied in Acadia National Park during 1992-1994 to evaluate causes of mortality, fecundity rates, yearling and adult survival rates, fawn survival rates, movements, habitat selection, and spatial interactions with roads, developed areas, and coyote territories. Twenty-seven fawns and sixteen adult deer were equipped with radio collared and monitored during the course of this study. The age structure of yearling and adult deer on MDI was comparable to an adjacent mainland population. However, survival rates of juvenile and older deer suggested that both recruitment and survival were likely insufficient to maintain the deer population at levels observed during the 1990's, despite that populations were already lower than reported in the 1960's. Both predation of coyotes on deer fawns and vehicular collisions with juvenile and adult deer were identified as likely factors limiting population growth of the deer herd within the eastern half of Acadia National Park. Home ranges of doe-fawns groups overlapped coyote territories extensively and there were high densities of coyote locations observed within the home ranges of radio collared fawns. Movement analyses indicated that home range areas of yearling and adult does on MDI were relatively large, and that home range and individual radio locations of collared deer occurred primarily within the park. Home range areas were larger during winter, but we observed neither seasonal shifts to lowland conifer habitats nor seasonal movement to wintering areas during the relatively mild winters which occurred during our study. Deer selected home ranges with disproportionately greater amounts of birch-aspen forest than occurred on the island suggesting an affinity for habitats burned during the 1947 fire. Within their home ranges, deer preferred deciduous forest stands based on higher browse availability. Positioning of deer home ranges did not appear to be influenced by road density, and within their home ranges deer movement did not appear to be affected by proximity to roads. Deer showed a weak attraction for areas of human development within their home

ranges. These results suggest a high potential for interaction of deer with vehicles, humans, and coyotes within the eastern portion of ANP. We make several recommendations for future monitoring of deer population within ANP and for the increased management of deer-vehicle interactions on MDI.

INTRODUCTION

White-tailed deer (*Odocoileus virginianus*) populations across much of North America occur at densities greater than those present in 1900 (deCalesta 1997, Knox 1997, Rooney 2001). The overabundance of deer is of great concern in National parks, particularly in the eastern United States (Porter 1992) where extirpation of large mammalian predators such as wolves (*Canis lupus*) and mountain lions (*Felis concolor*) (Nowak 1974, Dixon 1982, McCullough 1997), coupled with human enhanced food sources adjacent to parks, and protection from human hunting within parks, has resulted in irruptive populations in many deer populations associated with parks (Frost et al. 1997, Underwood and Porter 1997a). Additional causes for over abundance of deer in protected areas include habitat alterations such as fire, wind, flooding, or metapopulation processes that restrict or eliminate typical dispersal and source-sink dynamics (McCullough 1997).

Irruptions followed by periods of population decline have been documented for white-tailed deer on Mount Desert Island (MDI), Maine. The first documented population irruption occurred as early as 1880 on MDI (Leopold et al. 1947). In 1937 there were signs of over browsing by deer (Holmes 1944) and by 1939 it was suggested that deer browsing was interfering with natural plant succession (Aldous and Pearce 1939). The deer population was at a high during 1938-1940 (Goodrum 1945), and was estimated at 2,303 in 1940 (Favour 1942). In 1942 the MDI deer population was estimated at 2,300, and it was estimated that the forage supply could only support 1,200 deer (Holmes 1944). In 1945, Goodrum (1945) reported that preferred browse was limiting during winter as evidenced by deer foraging on less preferred species and suggested that the island supported the maximum number of deer for the food supply. Two years later (in 1947) a fire burned 29% (41 km²) of Acadia National Park (ANP). The deer

population was estimated at 400-500 in 1948 because of deer deaths associated with the fire and past over browsing, but the population increased to ca. 3,000 in the late 1950's resulting from increased browse availability following the fire (Shaw 1985). Deer existed at high densities throughout the 1950's to early 1960's, which resulted in widespread over browsing (Doudna 1954, Favour 1957). There were 29 deer mortalities documented to be caused by malnutrition during the winter of 1956, which led Banasiak (1956) to recommend that a herd reduction program be initiated. Similarly, many other eastern National Parks were experienced irrupting deer populations during the early 1960's (Porter and Underwood 1999) and ANP was no exception. Public hunting had not been allowed on MDI since 1905 (McLaughlin 1968), but 785 deer were removed during 1960-1967 by state and park officials in an attempt to reduce the deer population (McLaughlin 1968). There have been no reports of widespread over browsing by deer since the late 1960's (McLaughlin 1968, Allen 1970, Gilbert and Harrison 1982, Saeki 1991).

The National Park Service is mandated to maintain intact ecological communities under The Organic Act of 1916 (Keiter 1988). The insularization of National Parks (Burch 1988) and the effects of human populations on ecological communities adjacent to park borders have altered the function of many park ecosystems (Johnson and Agee 1988). Foraging by ungulates has both direct and indirect effects on plant and animal communities, and deer can act as a keystone herbivore by restructuring entire ecological communities (Waller and Alverson 1997, Paine 2000, Rooney 2001). Browsing by deer often results in local extinction of some species of plants and can cause shifts in the species composition of forest communities (Klein 1981, Rooney 2001). Further, continued over browsing can reduce plant cover and diversity and alter nutrient and carbon cycling (Côté et al. 2004), affect insect species diversity (Haddad et al. 2001), and

reduce the abundance and diversity of shrub-nesting birds (deCalesta 1994). Herbs are particularly vulnerable to browsing because they do not grow large enough to escape browsing pressure (Rooney and Waller 2003). Vascular plants and insects represent 70% of all described species (Wilson 1988), thus high deer densities are a potential threat to biological diversity. Species composition and vegetation structure has been severely altered in several eastern parks (Cypher et al. 1985, Sayre and Christie 1988, O'Connell 1989, Storm et al. 1989, Palmer et al. 1997, Underwood and Porter 1997b). Activities adjacent to park borders including suburbanization, agriculture, ornamental plantings, timber harvesting, and the resulting effects of increased edge and interspersions of habitats have increased the suitability of habitats for deer adjacent to parks and have enhanced the growth of deer populations (Soukup et al. 1990, Porter 1991). These activities have made managing deer populations within parks increasingly challenging. For example, residents of Mount Desert Island that are adjacent to ANP often complain that deer from the park are damaging ornamental trees and gardens and there is concern that high deer densities will transmit diseases via the deer tick (*Ixodes scapularis*). Minimizing conflict between white-tailed deer and other natural resources is a challenge to managers of public lands (Porter 1991, deCalesta 1997, Palmer 1997) and were of direct relevance when the decision to initiate this study occurred in 1990.

Acadia National Park has potential for significant effects of deer on vegetative succession, structure, and composition because of the park's small size and the large amount of boundary associated with private lands within the park (approximately half of Mount Desert Island is privately owned). Additionally, Mount Desert Island is connected to the mainland by a 0.6-km bridge, creating a relatively closed deer population, which eliminates emigration as a potential intrinsic population control (McCullough 1997) when density-dependent competition and

associated damage to vegetation may occur. Further, the fire of 1947 provided increased food supply, increased population densities of deer, and the potential for overbrowsing effects on post-fire succession (McLaughlin 1968). The Park Service has long been concerned that deer have the potential to alter post-fire plant succession (National Park Service 1982), particularly within ANP.

Deer populations on Mount Desert Island should be limited by food resources because of limited immigration and emigration, lack of hunting, and an altered predator community. However, ANP is an exception to the problem of overabundance. Studies of deer-vegetation interactions on MDI have suggested that since 1968, there is no evidence of overbrowsing by deer (McLaughlin 1968, Gilbert and Harrison 1982, Saeki 1991), except in localized wintering areas (McLaughlin 1968, Allen 1970). Vegetation in Acadia National Park has high dietary quality, yet utilization of preferred browse species declined from 1980 – 1989 with no change in browse availability, suggesting that deer populations have declined since 1980 (Saeki 1991). Further, MDI maintains higher levels of fecal crude protein for deer than occurred in a nearby mainland deer population that was hunted, suggesting that the MDI deer population was below K-carrying capacity during the late 1980's and early 1990's (Saeki 1991). Thus, previous work suggests that the declining deer population on MDI at that time that this study was initiated was caused by limiting factors other than nutritional and food limitations (Saeki 1991).

Predation can be an important factor in ungulate population dynamics (Gasaway et al. 1983, Messier and Cr te 1985) and the insular nature of MDI provides an opportunity to investigate whether predators are a regulating influence on deer populations. Potential predators of white-tailed deer on MDI include red foxes (*Vulpes vulpes*), bobcats (*Felis rufus*), and coyotes (*Canis latrans*) (Winter 1990, O'Connell et al. 1992). Bobcats are extremely uncommon and

reproducing populations are likely absent from ANP (Fuller and Harrison 2003). Further, bobcats were only an occasional predator of deer in Maine (Major and Sherburne 1987, Litvaitis and Harrison 1989). Red foxes are common in ANP, and white-tailed deer occurred in 26% of fox scats during summer (Fuller and Harrison 2003). However, foxes were not a documented cause of mortality of white-tailed deer fawns on MDI (Long et al. 1998). White-tailed deer remains were found in fox scats in Michigan, but Ozoga et al. (1982) suggested that fawn remains in scats may indicate scavenging and not necessarily kills. Although red fox are common, fox are probably not a major mortality source of the deer population on MDI. Fishers (*Martes pennanti*) are present, but are uncommon on MDI (Fuller and Harrison 2003) and are not considered a significant predator on deer (Arthur 1987, Douglas and Strickland 1987).

Eastern coyotes are a significant predator of white-tailed deer in Maine (Hilton 1978, Caturano 1983, Harrison and Harrison 1984, Major and Sherburne 1987, Litvaitis and Harrison 1989, Fuller and Harrison 2003) and elsewhere (Cook et al. 1971, Lingle 2000). Coyote predation is a major source of mortality for both adult deer (Hilton 1978, Bowen 1981, Gese and Grothe 1995, Whitlaw et al. 1998, Patterson et al. 2002) and fawns (Ballard et al. 1999, Patterson and Messier 2003). Coyotes are presently common on MDI, but only recently colonized the island in the early 1980's (Coman 1987, Winter 1990). For example, during the winters of 1979 and 1980, no coyotes were detected on 91 km of snow track surveys in ANP (Gilbert and Harrison 1982). During June and July, 86% of scats from coyote pups in Maine contained white-tailed deer remains (Harrison and Harrison 1984), while on MDI, 56% of scats from adult (> 1 year) coyotes contained deer remains (Fuller and Harrison 2003). The greatest source of adult deer mortality in northern New Brunswick, Canada was coyote predation (Whitlaw et al. 1998) and Harrison and Harrison (1984) suggested that adult coyotes prey on deer when pups are

weaned because of increased foraging efficiency of large prey when the protein demands of growing pups are high. On MDI, 47% of all fawn mortalities were attributed to coyote predation (Long et al. 1998). Coyotes are the largest predator on MDI, and represent the greatest potential source of natural mortality of the deer population when food is not limiting.

Domestic dogs were not a large cause of deer deaths in several studies (Progulske and Baskett 1958, Sweeney et al. 1971, Causey and Cude 1980), yet dogs are occasionally predators of newborn fawns (Lowry and McArthur 1978, Nelson and Woolf 1987, Fuller 1990, Decker et al. 1992, Long et al. 1998). In New Hampshire, dogs were the cause of 13.4% of reported deer kills between 1945 – 1962, and more than 400 kills each year in Vermont were attributed to dogs (<50 were attributed to coyotes and bobcats at that time) (Mattfeld 1984). Although unleashed dogs are not allowed in ANP, carriage roads and hiking trails are often used by visitors with unleashed dogs, which causes potential for significant interactions between dogs and deer.

Visitors to Acadia National Park and densities of residents on Mount Desert Island have been increasing and the influence of anthropogenic activities within and adjacent to the park may be a significant mortality factor for the deer population on MDI. Poaching, road kills, and predation by dogs accounted for 29% of mortalities of radio collared deer in Minnesota (Fuller 1990). Researchers suggest that mortality of ungulates resulting from human causes may be additive to natural predation by large carnivores (Gasaway et al. 1983, Peterson 1988).

Correspondingly, mortality from collisions with vehicles can be a substantial source of mortality for deer populations (Puglisi et al. 1974, Schaffer and Penland 1985, O’Gara and Harris 1988). Deer mortality from vehicles was responsible for 87% of the annual mortality at Valley Forge National Historical Park in Pennsylvania (Cypher et al. 1985). On MDI, collisions with vehicles accounted for 18% of the mortalities observed for white-tailed deer fawns, and was

second in prevalence to predation (Long et al. 1998). Deer mortality on MDI has been documented since the late 1930's when 112 deer were reported killed from 1938-1943 (Goodrum 1944) and there were 200 deer hit and killed during a 4-month period in 1960 during a high in the deer population (Shaw 1985). More recently, there were 179 accidents involving deer reported to the Town of Mount Desert police from 2000-2005. Increasing deer vehicle collisions create socioeconomic problems related to human health and safety and increasing trends in visitation rates to ANP had increased potential for deer collisions with vehicles when this study was initiated.

Additional to understanding potential sources of mortality of deer, it is important to evaluate habitat selection to evaluate why deer activities may be concentrated in particular habitats within ANP and adjacent nonpark lands. White-tailed deer use available habitat based on meeting requirements for food, rumination, movement, social interactions, and rest (Beier and McCullough 1990). Habitat selection during summer is usually based on the presence of digestible forage (Pauley et al. 1993), whereas deer use overstory types with closed canopies that provide snow interception during winters with significant snow cover (Banasiak 1961, Telfer 1970, Drolet 1976, Moen 1978). When snow accumulations exceeded 40 cm, white-tailed deer in northern Idaho selected overstory types with the least snow to minimize energy expenditure because of the reduced forage availability, reduced movement, and increased energetic costs associated with travel in deep snow (Pauley et al. 1993). Because of lower average snow depths on MDI, deer may respond differently to habitat selection during winter than deer within mainland sites in Maine.

The objectives of this study were to: 1) estimate cause-specific mortality rates of deer and to evaluate the potential influence of competing mortality factors on deer populations on MDI

during the period 1992-1994; 2) to evaluate seasonal habitat selection by deer on MDI; 3) to evaluate the extent to which radio collared deer used park and non-park lands; and 4) to evaluate the spatial relationships among deer home ranges and radio locations with roads, developed areas, coyote territories, and areas of high elevation within the park. We used observed mortality and fecundity data for deer on MDI to deterministically model influences of natural predation and human-caused mortality on the deer population in Acadia National Park. Our models were used to estimate the adult female survival rate and reproductive rates necessary to maintain a stable population. We also evaluated movements of deer to assess habitat selection, edge relationships, and potential for interactions with human, vehicles, and coyotes.

METHODS

Study Area

The study was centered within Acadia National Park on Mount Desert Island, Maine. The island is 280 km², and approximately 49% of the island is comprised of Acadia National Park. The island is divided into eastern and western portions by a 10-km-long fjord that is oriented north to south. The island includes glaciated valleys and granite mountains oriented from north to south, with elevations ranging from sea level to 466 m. Yearly visitation rates to the park are estimated at 2.7 million people (average 1994 through 1999) with visits peaking during summer (U.S. Department of the Interior 2000). Acadia National Park is ranked number 30 in visitation rates out of 353 National Parks (www2.nature.nps.gov/stats/).

Coniferous tree species on MDI include *Picea rubens*, *P. glauca*, *P. mariana*, *Abies balsamea*, *Larix laricina*, *Thuja occidentalis*, *Tsuga canadensis*, *Pinus rigida*, *P. strobus*, *P. resinosa*, and *P. banksiana*. Deciduous tree species include *Fagus grandifolia*, *Betula alleghaniensis*, *B. papyifera*, *B. populifolia*, *Acer saccharum*, *A. rubrum*, *Populus tremuloides*,

and *P. grandidentata*. The island was composed of 41% deciduous forest, 33% coniferous forest, 10% mixed coniferous-deciduous forest, 7% developed (business and residential) areas, 6% wetlands, and 3% unforested lands (e.g., shoreline and mountaintops) in 1979 (Figure 1); overstory composition changed little between that survey and the initiation of our study. In 1947 a fire burned 6,880 ha of the northeastern portion of the island (4,117 ha in ANP); by 1979, deciduous tree species dominated the forest overstory in previously burned areas (Figure 1). Mean monthly snowfall in ANP during the study was 28 cm, and the mean maximum depth of snow was 26 cm (National Oceanic and Atmospheric Administration 1992, 1993, 1994).

Capture and Radiotelemetry

Deer were captured during 1992 – 1994 in modified Clover traps (Clover 1954, McCullough 1975) or were darted with drug-injecting darts (Nelson and Mech 1981) fired from a capture gun. Traps were baited with alfalfa hay, commercial horse feed, white cedar, or apples and were checked at least twice daily. Captured deer were manually restrained and immobilized with an intramuscular injection of 100 mg xylazine (Rompun[®], Miles, Inc., Shawnee Mission, Kansas)/300 mg ketamine hydrochloride (Ketaset[®], Aveco Co., Inc., Fort Dodge, Iowa) and were fitted with radio collars (Advanced Telemetry Systems, Isanti, Minnesota, and Telonics, Inc., Mesa, Arizona). A first incisor was extracted in the field for use in determining age from cementum annuli (Gilbert 1966, Ransome 1966, Thomas and Bandy 1973). Deer were classified as fawns (6-12 months of age), yearlings (>12 and <24 months of age), or adults (\geq 24 months old) based on dental characteristics (Severinghaus 1949), cementum annuli, body size, shape and length of head, and presence or absence of antlers. Deer were fitted with a numbered, self-piercing ear tag (National Band and Tag Company, Newport, Kentucky) and a colored vinyl ear tag (Nasco, Inc., Fort Atkinson, Wisconsin). Deer were released at the site of capture following

an intramuscular injection (3.0 mg) of yohimbine (Yobine[®], Lloyd Laboratories, Shenandoah, IA) to reverse the effects of xylazine. Each radio collared deer was located $\geq 2 - 3$ times per week using a hand-held, 2-element directional antenna.

Age Structure

We estimated the age structure of the deer population on MDI using ages from radio collared deer and deer killed in collisions with vehicles. Similar to radio collared animals, deer that were killed by vehicles were subsequently aged via a combination of tooth eruption patterns and wear, cementum annuli, and morphological characteristics.

Home Range and Habitat Selection

Home ranges

Adaptive kernel (AK) home ranges (95%) (Worton 1989) were calculated based on deer that had a minimum of 45 radiolocations during summer or winter. To evaluate the extent that collared deer used park versus nonpark lands, we calculated the percent of radiolocations for each deer that were within Acadia National Park, and the percent of the home range of each deer that was within ANP.

Stand-scale habitat selection

Landcover categories considered in analysis of stand-scale habitat selection included 4 forest types including deciduous, coniferous, mixed deciduous-coniferous, and birch/aspen forests, as well as unforested areas (e.g., rocks, mountaintops, shoreline), and developed areas (residential or commercial). We subsequently omitted the mixed-deciduous type because it comprised only 6.8% of the study area and was absent from home ranges of all radio-collared deer. We evaluated stand-scale selection (i.e., 3rd order, *sensu* Johnson 1980) for the remaining overstory types within home ranges, using the individual deer as the sampling unit. Use of each overstory

type was defined as the proportion of locations in each overstory type, and availability was defined as the proportion of each overstory type within the home range of each individual. We calculated a selection index for each deer as use (U) minus availability (A) divided by availability ($[U-A]/A$) (Manly et al. 1993). We used a nonparametric Friedman's analysis of variance (ANOVA) to test whether deer used overstory types in proportion to availability within their home ranges (Conover 1980, Alldredge and Ratti 1986). If deer used overstory types disproportionate from availability, we used Fisher's least significant difference (LSD) procedure on the ranks of the selection indices for each deer, to determine which overstory types differed (Conover 1980, Alldredge and Ratti 1986). We used a pairwise rejection level of α/k , where $\alpha = 0.10$, and $k = 10$ possible comparisons (Miller 1981). We used a MANOVA to test for difference in selection of overstory types between males and females, using the selection index for each overstory type as the multiple dependent variables. If we did not detect a sex effect, we combined males and females in the analysis of stand-scale selection.

Landscape-scale habitat selection

We evaluated landscape-scale habitat selection (i.e., 2nd order, *sensu* Johnson 1980) by comparing the composition of overstory types within home ranges (use) with the composition of overstory types available to deer on MDI (availability). Since deer were not captured on the western side of MDI, availability was defined as the eastern portion of MDI. We calculated a selection index for each deer as use (U) minus availability (A) divided by availability ($[U-A]/A$) (Manly et al. 1993), and used the same statistical procedures used in the stand-scale habitat selection analyses (Friedman's ANOVA, Fisher's LSD, MANOVA).

Fawn and Coyote Overlap

We evaluated the relative potential for interaction between coyotes and deer fawns by calculating the percent of fawn radio locations that were within coyote territories. We also calculated the density of coyote radio locations within doe-fawn family groups and the percent overlap of doe-fawn family groups with coyote territories. Detailed methods on coyote home range estimation are in Fuller and Harrison (2006).

Road and Edge Associations

We calculated the density of roads (km/km^2) within each deer home range, and then compared to the road density within the area available to each deer within the eastern portion of MDI. For this landscape-scale road-density analysis we plotted mean density of roads within home ranges of females during summer and winter, and within yearly female and male home ranges. We also evaluated edge relationships by computing the distance between every deer radio location to the nearest developed area and to the nearest road (observed). To test for stand-scale edge selection or avoidance by deer, we compared observed mean distance to developed areas or the nearest road to the mean expected (i.e., average distance for the entire home range) distance within the home range of each deer to the nearest road or developed area using a Wilcoxon signed-rank test (Conover 1980). For the landscape-scale edge analysis we compared the mean distance to developed areas and roads within each deer home range to the mean distance to the nearest developed area or road within the eastern portion of MDI.

Elevation

Similarly to the methods used for our edge analyses, we compared the mean elevation within deer 95% AK home ranges to the mean elevation of deer radio locations within home ranges to determine if deer exhibit stand-scale selection for areas of relatively higher or lower elevations than expected. We used a Wilcoxon signed-rank test (Conover 1980) to compare observed and

expected elevations, using the individual deer as the unit of replication. We compared mean elevation within home ranges to elevation of observed locations for females during summer and winter, and for yearly home ranges of males and females (i.e., pooled across sexes)..

We also evaluated choices in elevation at a landscape-scale by comparing the mean elevation within home ranges to the mean elevation within the eastern portion of MDI. We determined differences by plotting means ± 2 standard errors of elevation within home ranges compared to the mean elevation across the eastern portion of MDI.

Survival

Causes of mortality were determined by examining characteristics of wounds, the death site, carcass location, and signs of predation or scavenging (scats, tracks, hair). Carcasses with puncture wounds on the head or neck with evidence of hemorrhage were classified as coyote predation (Cook et al. 1971). Carcasses with an undetermined cause of death were necropsied.

Survival rates of adult female deer were estimated using the Heisey and Fuller (1985) method, which extrapolates daily survival rates to longer intervals (Trent and Rongstad 1974). The year was divided into three intervals (Summer = May-September, Fall = October-December, Winter = January-April) in which constant daily survival (\hat{S}_i) and cause-specific mortality rates were assumed to remain constant. The method also assumes that all individuals within a class have the same survival and mortality probabilities. Because we had too few deer to test for annual variation, we pooled survival data across three years of the study (1992 – 1994).

Population Model

Our objective was to determine whether the deer that we sampled on MDI exhibited demographic characteristics consistent with a population that was stable, increasing, or

decreasing. We estimated the survival rate needed to maintain a population with an annual finite rate of population change equal to 1.0 using equation (1) in Henny et al. (1970:691):

$$1 = m_1 S_0 (\lambda)^{-1} + m_2 S_0 S_1 (\lambda)^{-2} + m_3 S_1 S_2 (\lambda)^{-3} + \dots,$$

where: m_x = age-specific birth rate of female fawns per adult female per year, S_x = age-specific female survival rate, and λ = the finite rate of population change. We assumed a constant survival rate beyond age 2, all does produced first fawns at 1 year, and a primary sex ratio of 1:1. The above equation was reduced to the following when adapted for deer populations using a Taylor series expansion:

$$1.0 = \frac{m_1 S_0}{\lambda} + \frac{m_2 S_0}{\lambda - S}$$

where: m_1 = mean birth rate of female fawns per juvenile female (1 – 2 years), m_2 = mean birth rate of female fawns per adult female (≥ 2 years), S_0 = annual survival rate of female fawns (≤ 1 year), and S = annual survival rate for yearling and adult females (> 1 year). We solved for S to determine the annual survival rate of females > 1 year needed to maintain a stationary population ($\lambda = 1$) given our estimates of birth rate and fawn survival:

$$S = \frac{\lambda - m_2 S_0}{1 - \frac{m_1 S_0}{\lambda}}$$

We estimated the annual birth rate of adults (ARR) and yearlings (YRR) using regression equations developed by Chilelli (1988) for deer in Maine:

$$\text{ARR} = 0.967 + 0.042 (\text{YABD})$$

$$\text{YRR} = -0.039 + 0.073 (\text{YABD})$$

where: adults are ≥ 3 years old at parturition, and yearlings are 2 years old at parturition; YABD = Yearling Antler Beam Diameter from previous November harvest.

We used mean antler beam diameters from Deer Management District 16 (DMD 16), which is the mainland district adjacent to MDI (Figure 2). The Maine Department of Inland Fisheries and Wildlife sampled 20 – 30% of the harvest each year in each deer management district (Lavigne 1993). We averaged the annual birth rates from 1992 – 1994, and assumed that 47% of fawns born are female (McCullough 1979, G. Lavigne, unpublished data). Thus, to calculate mean birth rates, we multiplied mean annual birth rates of adults and yearlings by 0.47 to arrive at the number of female fawns birthed per female adult or yearling. To determine if the frequency of yearling does on MDI was similar to the frequency of yearlings examined in the biological sample of DMD 16, we compared the proportion of yearlings in MDI vs. DMD 16 with a Z-test (Zar 1999).

We estimated the number of does that must be born per breeding-age doe to maintain a stable population using the following formula:

$$\bar{m} = \frac{1 - s}{s_0(1 - s + s_1)}$$

where: \bar{m} is the average number of female fawns birthed per breeding-age female, $2\bar{m}$ is thus the total number of fawns birthed per breeding-age female, assuming an equal sex ratio of fawns; s is the third-year and later annual survival rate; s_0 is the first-year survival rate; and s_1 is the second-year survival rate (Henney et al. 1970:694). This formula assumes a stable age distribution and that all females are pregnant and carry embryos to parturition at age 2 and beyond. This unrealistic assumption likely caused all of our estimates of birth rate needed to maintain a stable population to be optimistically low. We followed the method of VanCamp and Henny (1975), and used only a first-year survival rate and a constant annual survival rate for deer > 1 year of age.. We compared minimum birth rates required to maintain a stable

population by using survival rates estimated from deer on MDI ($\pm 95\%$ confidence interval), from the mainland deer population in DMD 16 (L. Cantor, Maine Department of Inland Fisheries and Wildlife, unpublished data), and from survival rates estimated in northern New Brunswick (Whitlaw et al. 1998).

RESULTS

Capture

Twenty-seven fawns were captured and monitored. Complete methods and results of the fawn capture and survival portion of the study were reported by Long et al. (1998). Sixteen deer (≥ 12 months) were captured and radio collared (5 M, 11 F). Of the males, 2 were adults (≥ 24 months), 1 was a yearling, and 2 were in undetermined age but > 1 year-old.. Of the females, 10 were adults and 1 was a yearling. Radio locations totaled 767 during the summer ($\bar{x} = 153/\text{individual}$) and 454 during winter ($\bar{x} = 90/\text{individual}$).

Age Structure

Based on the sample of captured and road-killed individuals, the average age of non-juvenile deer (> 2 years) on MDI was 5 years for males ($n = 10$) and 7 years for females ($n = 19$). The oldest known male deer that was aged was estimated at 14.5 years old, while the oldest female was 14 years. There was a greater proportion of male than female fawns, but the proportion of males and females were similar for yearlings (Figure 3). The older age classes of the population that we sampled were skewed towards females (Figure 3).

Home Range & Habitat Selection

Home ranges

Radiolocations totaled 767 during the summer and 454 during winter. The mean winter home-range area (95% adaptive kernel) for females (3.15 km^2 , $n = 4$) was > 2 times larger than

the mean area of their summer home ranges (1.45 km^2 , $n = 5$). Yearly home-range area for males ($\bar{X} = 6.62 \text{ km}^2$, $n = 3$) was nearly 3 times larger than for females ($\bar{X} = 2.22 \text{ km}^2$, $n = 6$). There was only one male with enough locations during the winter to calculate a home range; the area of his winter home range was 2.36 km^2 .

Based on the pooling of all radio locations during both summer and winter seasons (1992 – 1994), 92% were within ANP (Figure 7). For females, 96% of locations during summer ($n = 5$ individuals) and 95% ($n = 4$ individuals) of locations during winter were within the boundaries of ANP. Acadia National Park composes 61% of the eastern portion of MDI, and greater than 70% of the home ranges for all deer that we monitored were within the boundaries of ANP (Females summer = 94% [Figure 4], females winter = 87% [Figure 5], females yearly = 79%, males yearly = 71% [Figure 6]). Our results should be interpreted with caution, however, because the observed home ranges of collared deer comprised only 5.55% of the eastern portion of ANP during the summer and 9.91% of the eastern portion of ANP during winter.

Stand-scale habitat selection

Yearly selection indices for the 5 overstory types did not differ (Wilks' lambda = 0.425, $P = 0.610$) between males ($n = 3$) and females ($n = 6$); therefore, we combined sexes for yearly stand-scale analyses. Deer used overstory types disproportionate from availability within their home ranges ($P = 0.048$). Deciduous stands had the greatest relative preference, and selection of deciduous stands was significantly greater than for unforested ($P = 0.001$) and developed ($P = 0.002$) stands (pairwise rejection level = 0.01) (Table 1). There were no other significant differences among all other pairwise comparisons (Table 1).

There were no males with enough locations to determine a home range during the summer, and only one male with a winter home range, so seasonal habitat selection could only be

Table 1. Multiple pairwise comparisons between rank sums^a of selection indices among 5 overstory types for yearly stand-scale habitat selection of white-tailed deer (n = 6 F, 3 M), Mount Desert Island, Maine, 1992 – 1994. Habitat types were ranked from lowest selection index (1) to highest (5) for each deer and then summed across all deer.

Overstory Type	Rank Sum	vs.	Overstory Type	Rank Sum	P-value ^b
Deciduous	36		Birch/Aspen	30	0.278
Deciduous	36		Coniferous	30	0.278
Deciduous	36		Unforested	21	0.009
Deciduous	36		Developed	18	0.002
Birch/Aspen	30		Coniferous	30	1.000
Birch/Aspen	30		Unforested	21	0.107
Birch/Aspen	30		Developed	18	0.034
Coniferous	30		Unforested	21	0.107
Coniferous	30		Developed	18	0.034
Unforested	21		Developed	18	0.585

^a Sum of rank of habitat selection indices among 5 overstory types.

^b Bonferroni pairwise rejection level = 0.01 ($\alpha = 0.10$, 10 comparisons). Significant differences are depicted in bold.

evaluated for females. Female deer ($n = 5$) used overstory types disproportionate from availability within their home ranges during the summer ($F = 7.84$, $P = 0.098$). Coniferous stands had the highest relative preference during summer, and selection of coniferous stands was significantly greater than for developed stands ($P = 0.003$, pairwise rejection level = 0.01). No other pairwise differences in selection indices were significant during the summer. During the winter, female deer ($n = 4$) were not selective in their use of overstory types ($F = 7.15$, $P = 0.128$).

Landscape-scale habitat selection

Yearly landscape-scale selection indices did not differ between males ($n = 3$) and females ($n = 6$) (Wilk's Lambda = 0.278, $P = 0.379$), so we pooled sexes for analyses based on the home ranges of deer throughout the year. Based on those composite home ranges across both seasons, we observed landscape-scale selection by deer ($F = 15.29$, $P = 0.004$) (Figure 8). Birch/aspen forest had the highest selection index, which was significantly greater than indices for unforested land, developed areas, coniferous forest, and deciduous forest types ($P < 0.001$) (pairwise rejection level = 0.01) (Table 2). We also detected evidence for landscape-scale selection by female deer during summer ($F = 11.36$, $P = 0.023$) (Figure 9) and winter ($F = 9.40$, $P = 0.052$) (Figure 10). During both summer and winter, females selected birch/aspen forests at the landscape-scale over developed areas, deciduous forests, and coniferous forests ($P < 0.001$) (Figure 11).

Fawn and Coyote Overlap

Doe-fawn family-groups on the eastern portion of MDI included a group near Sand Beach fawns and a group located in the vicinity of Kebo Mountain and Great Meadow (Figure 12). Of all fawn locations, 93% were within a coyote territory (Figure 12). Density of coyote locations

Table 2. Multiple pairwise comparisons between rank sums^a of selection indices among 5 overstory types for yearly landscape-scale habitat selection of white-tailed deer (n = 6 F, 3 M), Mount Desert Island, Maine, 1992 – 1994. Habitat types were ranked from lowest selection index (1) to highest (5) for each deer and then summed across all deer.

Overstory Type	Rank Sum	vs.	Overstory Type	Rank Sum	P-value ^b
Birch/Aspen	43		Developed	25	0.0006
Birch/Aspen	43		Deciduous	19	0.0000
Birch/Aspen	43		Coniferous	23	0.0002
Birch/Aspen	43		Unforested	25	0.0006
Unforested	25		Developed	25	1.0000
Unforested	25		Deciduous	19	0.2211
Unforested	25		Coniferous	23	0.6808
Developed	25		Deciduous	19	0.2211
Developed	25		Coniferous	23	0.6808
Coniferous	23		Deciduous	19	0.4122

^a Sum of rank of habitat selection index among 5 overstory types.

^b Bonferroni pairwise rejection level = 0.01 ($\alpha = 0.10$, 10 comparisons). Significant differences are depicted in bold.

within the Sand Beach doe-fawn group was $4.34/\text{km}^2$, and was $3.66/\text{km}^2$ within the Kebo/Great Meadow fawn group. The composite home range of the Sand Beach doe-fawn group overlapped 100% with a coyote family territory that was centered around Otter Creek. The composite home range of the Kebo/Great Meadow doe-fawn group overlapped 64% with the family territory of the Otter Creek coyotes and 47% with the territory of a second family of coyotes near Aunt Betty pond (see Fuller and Harrison 2006 for information on coyote family territories on MDI).

Overall, 93% of the composite home range of the the Kebo/Great Meadow doe-fawn group overlapped with a coyote territory,

Road/Edge Associations

Density of roads within summer and winter home ranges of deer were similar (Figure 13). Road density within summer and winter deer home ranges did not differ from the density of roads within the eastern portion of MDI (Figure 13). However, mean road density within yearly home ranges (3.50 km^2) was 37% greater than the road density within the eastern portion of MDI (2.56 km^2).

Deer did not make stand-scale decisions suggesting either selection or avoidance of roads within their home ranges. Distance of deer locations to the nearest road (R) did not differ from the average distance within each deer home range (r) for females during the summer ($Z = 0.674$, $P = 0.500$, $n = 5$, $R = 133 \text{ m}$, $r = 138 \text{ m}$) or winter ($Z = 0.730$, $P = 0.465$, $n = 4$, $R = 132 \text{ m}$, $r = 157 \text{ m}$), for yearly home ranges of females ($Z = 0.315$, $P = 0.753$, $R = 121 \text{ m}$, $r = 127 \text{ m}$), or for yearly ranges of males and females combined ($Z = 1.362$, $P = 0.173$, $R = 129 \text{ m}$, $r = 143 \text{ m}$). Similarly, deer did not appear to be avoiding developed areas at the stand-scale. The mean distance of deer locations to developed areas (D) did not differ from the mean distance within deer home ranges (d) for females during the summer ($Z = 0.674$, $P = 0.500$, $n = 5$, $D = 386 \text{ m}$, d

= 398 m) or winter ($Z = 1.461$, $P = 0.144$, $n = 4$, $D = 424$ m, $d = 486$ m), or within the yearly home range of females ($Z = 0.944$, $P = 0.345$, $n = 6$, $D = 339$ m, $d = 342$ m). For females ($n = 6$) and males ($n = 3$) combined, mean distance of radiolocations within yearly home ranges to the nearest developed area ($\bar{X} = 330.27$ m) was significantly less than ($Z = 1.718$, $P = 0.086$) the mean distance within the home range to the nearest developed area ($\bar{X} = 353.26$ m), indicating that there was a spatial affinity between deer and development.

Elevation

Stand-scale movement decisions of deer did not appear to be strongly influenced by preferences for different elevations within their home ranges. There was no difference between the mean elevation within home ranges and actual radio locations of female deer within those home ranges during the summer ($Z = 0.135$, $P = 0.893$, $n = 5$) or winter ($Z = -0.365$, $P = 0.715$, $n = 4$), or within yearly home ranges of males and females combined ($Z = -1.362$, $P = 0.173$, $n = 9$). Mean elevation within deer home ranges of males and females combined was 51.1 m and the mean elevation of radiolocations within home ranges was 53.1 m.

Elevation within summer ($\bar{X} = 65.2$) and winter ($\bar{X} = 63.3$) home ranges of female deer did not differ from the elevation within the eastern portion of MDI ($\bar{X} = 84.8$ m) (Figures 14 & 15). However, elevation within yearly home ranges of males and females combined ($\bar{X} = 51.1$ m) was lower than the elevation within the eastern portion of MDI ($\bar{X} = 84.8$ m) (Figures 15 & 16), suggesting that deer may have been more likely to occupy home ranges at lower elevations (i.e., 2nd order selection), but used all elevations proportionally within their established home ranges (i.e., no 3rd order selection).

Survival

For all radio collared deer, sources of mortality included vehicle collisions ($n = 4$), predation ($n = 1$), and drowning ($n = 1$). Additionally, 3 deer died from complications associated with capture myopathy following their capture and restraint and their data was censored from further survival and modeling analyses. Yearly survival rates were estimated for female deer during the fall, summer, and autumn seasons based on 7 individuals that were monitored over 2,615 deer-days. We documented four mortalities of those does including 2 by vehicle collisions, 1 by coyote predation, and 1 by drowning. Survival rates were pooled for yearling and adult does and were highest during fall ($\hat{S}_i = 1.00$), and declined during summer ($\hat{S}_i = 0.88$) and winter ($\hat{S}_i = 0.67$) (Table 3). Estimated yearly survival rate for 7 yearling/adult does was 0.59, and survival rate of female fawns to 1 year of age was 0.27 (Long et al. 1998).

During the study (1991 – 1994) there were 33 reports of deer hit by vehicles. The greatest number of collisions occurred during June – August ($n = 14$), followed by March – May ($n = 11$), September – November ($n = 7$), and December – February ($n = 1$). We were able to obtain sex and ages from 31 road-killed deer ($n = 11$ M, 20 F). Deer reported as road-kills included radio collared and non-radio collared deer. The proportion of yearlings in the road-killed sample was similar between males and females, but a greater proportion of older (8+ years) females were represented in the road-killed sample (Figure 17). Additionally, a greater proportion of male fawns were represented in the road-killed sample compared to female fawns (Figure 17).

Population Model

The average annual adult female birth rate that we estimated for Deer Management District 16 was 1.737, and the average annual yearling female birth rate was 1.299. Thus, the average number of female fawns birthed per adult female was estimated at 0.816, and the average number of female fawns birthed per yearling female was estimated at 0.611. Counts of

Table 3. Heisey-Fuller interval survival rates (\hat{S}_i) and survival rate over all I intervals (\hat{S}^*) for yearling and adult (≥ 1 year) female white-tailed deer on Mount Desert Island, Maine, 1992 – 1994.

Season	1992 – 1994 Pooled		n
	\hat{S}_i (95% CI)	Radio Days	
Summer (May-September)	0.88 (0.69-1.00)	1241	3
Fall (October-December)	1.00 (1.00-1.00)	481	2
Winter (January-April)	0.67 (0.42-1.00)	893	5
Yearly (\hat{S}^*) (January-December)	0.59 (0.35-0.99)	2615	7

female fawns fetuses per doe on MDI obtained via *in utero* examinations of deer were 0.88 for adult ($n = 8$) and 0.59 for yearling ($n = 4$) does, which suggests that the reproductive rates that we used were closely matched with the actual deer population on MDI. Further, the proportion of yearling does sampled on MDI (0.24, $n = 6$ yearlings, 1992 – 1994) did not differ ($Z = 0.222$, $P = 0.413$) from the proportion of does sampled by state biologists in DMD 16 (0.22, $n = 33$ yearlings, 1986 – 1993) (Figure 18).

The survival rate of fawns used to model the deer population within the eastern portion of MDI was obtained from a companion study by Long et al. (1998). Survival to 1 year of age was estimated as 0.27 (80% CI = 0.000 – 0.558). Using the estimates $s_0 = 0.27$, $m_1 = 0.611$, and $m_2 = 0.816$, the annual survival rate of yearling and adult females needed to maintain a population with $\lambda = 1$ was estimated as 0.933. Using the 80% upper confidence interval on estimated fawn survival (0.558), the annual survival rate of yearling and adult females would still need to be 0.826. The observed survival rate for our limited sample of radioed yearling and adult does on MDI was 0.59.

Using the formula from Henny et al. (1970), (and using the estimates s & $s_1 = 0.59$, $s_0 = 0.27$ [Long et al. 1998]) we estimated $\bar{m} = 1.52$, or $2\bar{m} = 3.04$, indicating that 3.04 fawns per breeding-age female would be required to maintain a stable population (Table 4). Our true estimates of adult birth rates on MDI (assuming an equal sex ratio of fawns) are $\bar{m} = 0.869$, and $2\bar{m} = 1.74$. Thus, given estimated birth rates on MDI, fecundity would have needed to increase by 43% to maintain a stable population at observed rates of yearling/adult doe survival. Given the wide confidence intervals on our estimates of survival, we also estimated \bar{m} and $2\bar{m}$ using an 80% confidence interval on fawn survival and a 95% confidence interval on adult survival (Table 4). Only when we used the upper 80% confidence interval on fawn survival (0.56) or the

Table 4. Annual birth rates of female fawns required per yearling and adult doe (\bar{m}) and total number of fawns of both sexes required to be birthed annually per yearling and adult doe ($2\bar{m}$) to maintain a stable population under different survival rate scenarios on Mount Desert Island, Maine.

s & s_1 ^a	s_0 ^b	\bar{m} ^c	$2\bar{m}$ ^d
0.59 (actual)	0.27 (actual)	1.52	3.04
0.59 (actual)	0.56 (80% CI Upper)	0.74	1.47
0.35 (95% CI Lower)	0.27 (actual)	2.41	4.82
0.99 (95% CI Upper)	0.27 (actual)	0.04	0.07
	Actual Values on MDI	0.87	1.74

^a Second year and later annual survival rate estimated on MDI = 0.59, 95% confidence interval = 0.35 – 0.99.

^b First year survival rate (Long et al. 1988) = 0.27, 80% confidence interval = 0.00 – 0.56.

^c Average number of fawns required to be birthed annually per breeding-age female.

^d Total number of fawns required to be birthed annually per breeding-age female.

95% upper confidence interval on adult survival, did the birth rate necessary for a stable population become feasible. Conversely, when we used the estimates for yearling and adult survival from the DMD 16 (s & $s_1 = 0.78$), along with the published estimate of first year fawn survival on MDI (0.27), 1.60 fawns per breeding-age female would be required to maintain a stable population, which still far exceeds birth rates observed for white-tailed deer populations in the northeast portion of the species' geographic range. Finally, when we used the yearling and adult female survival rates (s & $s_1 = 0.85$) observed during field studies conducted in New Brunswick (Whitlaw et al. 1998), along with published estimates of first year survival for MDI, we estimated that 1.08 female fawns per breeding-age female would be required to maintain a stable population, which still exceeds published birth rates observed in nearly all white-tailed deer populations.

DISCUSSION

Home-range areas used by deer on Mount Desert Island were considerably larger than those reported in previous studies. Average yearly home-range size of males (662 ha) on MDI was almost 3X that of females (222 ha), and home ranges of females during the winter (315 ha) were > 2X those of females during the summer (145 ha). Previous reports include estimates of 161 – 480 ha (Rongstad and Tester 1969) and 135 ha (Tierson et al. 1985) in winter, and summer home ranges reported vary from 83 – 319 ha (Nelson and Mech 1981), and were 225 ha in the Adirondacks of New York (Tierson et al. 1985). Yearly home ranges averaged 250 ha in South Dakota (Sparrowe and Springer 1970), and Marchington and Hirth (1984) reported deer home ranges from 59 – 520 ha. Density of deer on MDI during our study was likely below forage carrying capacity (Saeki 1991), thus deer do not appear to be spatially or nutritionally

(Saeki 1991) limited. We speculate that deer occurring at low density on MDI may lack the social pressures that would restrict doe-fawn groups to smaller home ranges at higher densities.

Habitat use by deer is greatly influenced by browse and cover availability. Deer optimize foraging efficiency by feeding on foods that offer the greatest nutrition per unit weight consumed (Allen 1968). At the landscape-scale, deer selected birch/aspen forests over all other land cover types, presumably because of the high quality and high relative preference of aspen and birch twigs (Saeki 1991). Landscape-scale habitat selection analyses of females during summer and winter indicate preference for birch/aspen forests over developed areas and over deciduous, and coniferous forests. Based on a preference index, the five most preferred species by deer on MDI were rose (*Rosa* spp.), serviceberry (*Amelanchier* spp.), red oak, big-tooth aspen (*Populus grandidentata*), and quaking aspen (Saeki 1991). When positioning home ranges on the landscape, deer on MDI are probably selecting overstory types that maximize energy intake from high quality browse.

Within yearly home ranges, deer selected deciduous stands over unforested and developed areas, again probably because of greater forage value (Table 1). Selection for deciduous stands (highest rank sum across all land cover types) at the stand-scale corresponds with the research by Saeki (1991) in which quaking aspen (*Populus tremuloides*), red oak (*Quercus rubra*), and red maple (*Acer rubrum*) were among the most highly utilized browse species by deer on MDI. Females did not exhibit selection for overstory types within home ranges at the stand-scale during the winter, but selected coniferous stands over developed stands during the summer. Deer in New Brunswick selected dense coniferous and mixed stands during winter when snow depths reached 38 cm in open overstory types (Telfer 1970), presumably to reduce energetic costs associated with travel in deep snow. Similarly, deer mobility was reduced in Ontario when snow

depths increased from 25 to 35 cm (Hepburn 1959). Mean monthly snowfall on MDI during the study was 28 cm, and the maximum snow depth was 86 cm during March 1993 (National Oceanic and Atmospheric Administration 1992, 1993, 1994). Because snowfall on Mount Desert Island is not typically as heavy as on the mainland, deer generally do not experience the greatly elevated energetic costs associated with moving through deep snow during the winter, thus, use of habitat types within the home ranges of deer was similar during both summer and winter. We expect that during severe winters, which were absent during our study, deer in ANP may exhibit more classical seasonal shifts in habitat selection towards more coniferous stands.

Deer did not appear to be making stand-scale movements with regards to road density, or distance to nearest roads. However, at the landscape-scale, density of roads was greater within yearly home ranges than the expected based on the density of roads within the eastern portion of MDI. In combination, those results suggest that home range placement of radio collared deer may elevate their risk of road mortality and that they do not exhibit finer scale avoidance of habitat near roads. Additionally, locations within yearly home ranges of males and females (pooled) were closer to developed areas than the average distance within their home range. The combined effects of those habitat decisions could potentially increase the potential for deer-vehicle interactions on the eastern side of MDI, and may increase the potential for other adverse deer-human interactions (e.g., browsing on ornamental plants and feeding in vegetable and flower gardens).

Deer-vehicle collisions are a serious threat to the deer population in Acadia National Park. Of the 6 non-capture-related mortalities that we observed of adult deer, 4 were caused by collisions with vehicles. Additionally, there were 33 reported deer hit by vehicles during the duration of our study (1991 – 1994). The greatest number of collisions occurred during June – August,

corresponding with the greatest visitation rates, and presumably traffic volumes, within the park. The number of road-killed deer is an underestimate because it only reflects the number of deer that were reported. Fawns and yearlings were most commonly killed by vehicles, as were females ≥ 8 years old. Similarly, a study conducted in Montana reported that automobiles killed more fawns and old-aged female deer (≥ 7 years old) (O’Gara and Harris 1988). Vinck (1993) reported an average of 50 deer vehicle accidents per year (1987 – 1992) on MDI, of which an average of 30 resulted in death. Additional to contributing to a potentially non-sustainable mortality rate for deer, the collisions between deer and vehicles result in property damage and occasionally severe human injuries. Therefore, management efforts to reduce the potential for deer-vehicle collisions should be a high priority of ANP. Low cost-programs to reduce deer-vehicle collisions include educating visitors about areas of elevated risks and time periods when deer collisions are more likely, as well as usual approaches such as erecting warning signs to identify deer-crossings (Romin and Bissonette 1996). Permanent deer-crossing signs are the most commonly attempted technique for reducing deer-vehicle collisions (Sullivan and Messmer 2003), but they are often not effective because motorists habituate to them (Hughes et al. 1996). Adult deer increase mobility and often extend home range boundaries during rut to maximize opportunities for breeding (Nelson and Mech 1981, Beier and McCullough 1990), so there may be increased risk of collisions during fall associated with greater movement across roads. Additionally, deer are most active at sunset and just after sunrise (Kammermeyer and Marchinton 1977, Beier and McCullough 1990), as indicated by peaks in deer/vehicle collisions at 7am and between 6 – 9 pm (Vinck 1993). Education as well as management of the areas with the greatest past incidences of deer/vehicle collisions could reduce the number of yearly deer deaths, which would potentially slow the apparent decline of the deer population on MDI (circa

1994). Finally, efforts to reduce vehicular traffic within ANP, such as the ongoing park and ride program should be further encouraged.

In general, deer occupied home ranges year-round in areas of lower average elevation relative to the mean elevation on the eastern portion of MDI. However, deer were not selective in regards to the elevations used within their home ranges. Again, the low density of deer on the eastern side of MDI may have allowed deer to selectively choose preferred areas where seasonal and daily selection for habitats in regard to elevation were not required. Correspondingly, we did not observe the classical seasonal movements to low elevation coniferous habitat exhibited by many northern deer populations.

Deer within Acadia National Park have positive, non-consumptive-use values associated with sightings by visitors, aesthetic, and altruistic values. Negative values associated with deer include damage resulting from deer-vehicle collisions, and deer damage to ornamental and vegetable gardens outside of the park. All deer home ranges were $> 70\%$ within Acadia National Park, thus $< 30\%$ of the home ranges of deer were outside of the park. Additionally, the vast majority of radio locations of male and female deer that we monitored were within the park. However, deer still venture to adjacent lands and cause damage to gardens and ornamental trees and we can not reasonably conclude based on our limited sample of radioed deer that some resident deer do not concentrate their activities near human-created food sources. Areas are more susceptible to deer damage when edges are present (Kay 1993, Reimoser and Gossow 1996), such as the edges that exist between park and non-park lands. Conover (1997) suggests that damage to household gardens should increase at a faster rate than deer population increase until the highly palatable crop is destroyed or entirely eaten. Unpalatable crops should have slight damage until the most palatable plants have already been eaten, at which point damage to

the less palatable plants should rapidly increase (Conover 1997). Thus, it is important to note that human-deer conflicts associated with damage to highly preferred foods (e.g., many ornamental shrubs, flowers, vegetables, and fruits) does not necessarily indicate that the deer population is exceeding the forage carrying capacity of their natural habitat (Smith and Coggin 1984).

Our population model suggests that the deer population on the east portion of Mount Desert Island was likely declining during our study. Yearly survival rate of adult female deer on MDI were only 0.59, which is much lower than those reported in other studies. For example, annual survival rates of adult female deer in Montana ranged from 0.45 – 0.81 over a 10 year period (Dusek et al. 1992), averaged 0.85 in northern New Brunswick (Whitlaw et al. 1998), and were 0.71 in north-central Minnesota (Fuller 1990). Adult female survival of 50% has been suggested to exceed the genetic capability of white-tailed deer to replace losses, leading to population extinction (McCullough 1979). It is also reported that deer populations that are not subjected to hunting or other additive sources of mortality can withstand a minimum of 82% survival rate (McCullough 1979). Additional to the low adult survival rates observed for our small radio collared sample of yearling and adult does within the eastern portion of MDI, the first-year survival rate of female fawns based on companion studies on MDI was only 0.27 (Long et al. 1998), which is also lower than reported in many other studies. Fawn survival from birth to 30 days was 0.34 in Colorado (Whittaker and Lindzey 1999) and survival from birth through October was 0.39 in Minnesota (Fuller 1990). However, annual survival of deer fawns in northern New Brunswick was comparable (0.23) (Ballard et al. 1999) to rates observed for MDI; however, observed survival rates of yearling and adult does were higher in New Brunswick. A stochastic population model for Maine's white-tailed deer population concluded that survival

rates had a greater influence on deer population growth than did reproductive rates (Chilelli 1988). Thus, the low survival rates observed for fawns and adults on MDI could be of concern because of potential limitations on the resulting rate of population change.

A study in Acadia National Park during the 1960's indicated that the deer population had recently decreased, and McLaughlin (1968) suggested that the pattern of decrease would continue. Based on fawn and adult survival rates for MDI, the population equation predicts that unreasonably high fecundity rates may be necessary to maintain populations at 1991-94 levels.. Using an adult and juvenile survival rate of 0.59 and a yearling survival rate of 0.27, we estimated that 3.04 fawns would be required per breeding-age female to maintain a stable population. The birth rate of 3.04 fawns per breeding-age female is an underestimate because it assumes that all breeding-age does have the same fecundity, but yearlings actually have ca. 25% lower fecundity than adults. Assuming an equal sex ratio of fawns, our true estimate of adult fecundity needed to maintain the population is 1.74 fawns birthed per female per year. Only when we use the 80% upper confidence interval on fawn survival (0.56) with the estimate of adult survival (0.59) did annual birth rates of fawns required to maintain a stable population become feasible (1.47). If the first year survival rate on MDI remained the same, but adult survival rates were increased to those observed in the mainland deer population in DMD 16 (0.78) or in northern New Brunswick (0.85), fecundity rates required to maintain a stable population would likely be attainable (1.60 fawns/doe and 1.08 fawns/doe, respectively) if habitat conditions continued to remain favorable.

Our population model also suggests that an unreasonably high adult-female survival rate would be needed to maintain a population with a finite rate of increase (λ) = 1. We estimated that the adult female survival rate must be 0.93 in order to maintain a population with $\lambda = 1$. The

actual adult female survival rate on MDI that we estimated was only 0.59, suggesting that if the fawn survival rate remains at 0.27, the population will continue to decrease. Even when we used the 80% upper confidence interval on fawn survival (0.56), adult female survival rate needed to maintain a stable population (0.83) was still greater than what we observed. The adult female survival rate with hunting mortality removed was 0.78 from the mainland DMD surrounding MDI (L. Cantor, Maine Department of Inland Fisheries and Wildlife, unpublished data), and was 0.85 in northern New Brunswick where doe harvest was illegal (Whitlaw et al. 1998). This suggests that even in areas that have stable deer populations, our population model based on data from MDI requires fawn survival rates at or above the 80% confidence interval of what we observed. Our population models suggest a declining deer population that only becomes stable if juvenile and adult survival increases, or if juvenile survival alone increases dramatically.

Fecundity patterns in white-tailed deer may differ based on available space, inter- and intraspecific interactions, and environmental conditions, including availability of nutritional forage, which may result in: (a) increased or decreased mean age at puberty; (b) increase or decrease in fecundity plateau by shifting pregnancy rates; or (c) increase or decrease in fecundity plateau by shifting mean litter size (Caughley 1976). Reduced reproductive rates due to nutritional stress have been documented when quantity or quality of forage is inadequate (Klein 1970), possibly producing decreased ovulation rates (Woolf and Harder 1979). A density-dependent population at carrying capacity would have little or no fawn recruitment, a near-zero rate of population growth, and overuse of food supplies (McCullough 1979). Fecundity rates on MDI were 1.88 fawns birthed per adult doe and 1.25 fawns birthed per yearling doe, similar to the average annual birth rate for DMD 16 (adults = 1.74, yearlings = 1.30). Further, the proportion of yearling does also did not differ between MDI (0.24) and DMD 16 (0.22). Embryo

counts for deer on MDI during the 1960's were 1.17 for yearlings and 1.65 for adults (McLaughlin 1968). The number of fawns per female in Minnesota averaged 1.40 (≥ 2.0 years) (Fuller 1990), and reproductive rates in southeastern Canada averaged 1.36 embryos per doe (Huot et al. 1984). Thus, the deer population on MDI has a vigorous fecundity rate suggesting that deer are not overusing the food supply, yet browsing surveys (Saeki 1991) and our results suggest that the population was declining during the late 1980's and early 1990's. All evidence for the declining deer population on MDI indicates that fawn and adult survival is the limiting factor. Food supply is adequate, fecundity rates are vigorous, but survival rates of all age cohorts appear low relative to stable or increasing populations studied elsewhere.

Habitat associations and population regulation theory in deer is usually assumed to follow a determinate carrying capacity, which is linked to forage availability through a density-dependent interaction (Caughley 1976, McCullough 1979); however, population regulation theories have been questioned as to the role of predation (Peek 1980, Gasaway et al. 1983). Predators can be a primary cause of ungulate-fawn mortality, may cause ungulate numbers to decline below carrying capacity, and may accelerate declines in ungulate populations due to other causes such as poor quality habitat (Connolly 1978). Eastern coyotes were new to MDI in the 1980's (Winter 1990), and are the largest and most common natural predator of deer on MDI. Deer represented a significant portion of the coyote diets on MDI during summer (56% of coyote scats on MDI contained deer remains) (Fuller and Harrison 2003), and annually (O'Connell et al. 1992). Further, coyotes caused 47% of all fawn mortalities on MDI (Long et al. 1998). Elsewhere, eastern coyotes kill fawns as well as deer in that were not at immediate risk of starvation, as indicated by $> 80\%$ femur marrow fat (Parker and Maxwell 1989, Lavigne 1992). Deer fawns accounted for 63% of the deer killed by coyotes in Quebec (Messier et al. 1986), and

coyote predation accounted for 79% of early fawn mortality for deer in Colorado (Whittaker and Lindzey 1999).

Pooling all radio locations of fawns across MDI, 93% occurred within a coyote territory, indicating significant potential for coyote predation on fawns. Additionally, of the two doe-fawn groups that we monitored, > 93% of their composite home ranges overlapped with coyote territories. The density of coyote locations within fawn groups ($3.7/\text{km}^2 - 4.3/\text{km}^2$) also suggested high potential levels for interaction between coyotes and deer fawns. Predator removal studies with the goal of increasing deer for game hunting have documented increased fawn:doe ratios after coyote reduction (Beason 1974, Stout 1982), with increases up to 262% following reduction (Stout 1982). However, only very intensive predator control programs would increase fawn:doe ratios. The National Park Service's natural resource policies for ANP attempt to "perpetuate the natural, cultural, and scenic resources of Acadia National Park" with an objective to "protect and manage the park's natural resources, giving priority to those that are exceptionally fragile or significant" (U.S. Department of the Interior 1992). Further, indigenous species on National Park Service lands may be actively managed as "pests" in order to 1) prevent the loss of another species, 2) preserve the integrity of cultural resources, and 3) protect human safety (USDI 1988). Thus, lethal control of coyotes is not a recommended solution to the apparently declining deer population (circa 1989-1994) within ANP.

Conclusions and Management Recommendations

Our research suggests, that with our observed estimates of fawn and adult doe survival, the deer population on MDI would be predicted to exhibit a decreasing population trajectory. That predicted decline, which is consistent with our observations and browse surveys during the late 1980's and early 1990's, suggest that declines were not attributable to a lack of high quality

forage, as documented by Saeki (1991). Our results suggest that the deer population was likely declining because of low fawn survival and low survival of yearling and adult does.

We recommend long-term monitoring of the deer population in ANP, increased attention to the adverse effects of deer-vehicle interactions on MDI, as well as enhanced education of the public about deer management issues:

- 1). We suggest periodic analysis of dietary quality in addition to surveys of deer density, browse availability, and browse utilization to monitor the deer population and deer habitat relationships in ANP (Fuller and Harrison 2003). Indicators of over browsing based on vegetation measurements will allow park biologists to monitor progress towards specific management goals.
- 2). Analysis of availability and utilization of preferred browse species and fecal crude protein as an index of dietary quality could provide a reliable index to the status of the deer population relative to forage carrying capacity (Fuller and Harrison 2003). Browse utilization and availability were measured in 1980 (Gilbert and Harrison 1982) and 1989 (Saeki 1991), and a baseline assessment of fecal crude protein was conducted (Saeki 1991). We suggest conducting browse surveys using the methods of Saeki (1991) at 10-year intervals and to repeated Saeki's protocol for monitoring fecal crude protein via pellet collects during late winter during period of deep snow when deer are not feeding heavily on acorns (which can confound results because of tannin ingestion). Given that the last browse survey and fecal crude protein surveys were conducted in 1989-90, we recommend that a new survey be conducted as soon as possible.
- 3). Despite our recommendations above, it should be recognized that analyses of dietary quality, including fecal crude protein do not track changes in density or distribution of

deer. Thus, replication of the snow surveys conducted in winters 1988 and 1989 within ANP and reported by Fuller and Harrison 2003 may be useful. Snow track transects could provide useful data on changes in the relative abundance and distribution of deer in ANP. However, counting pellets in conjunction with browse surveys would likely be more reliable and cost effective (Fuller and Harrison 2003).

4). The NPS established several exclosures for deer shortly following the 1947 fire to evaluate deer-vegetation interactions. On MDI, exclosures were resurveyed and reconstructed in the late 1980's near Precipice, Breakneck Ponds, Upper Hadlock Pond, Aunt Betty Pond, and Jordan Pond. Results and analyses of past surveys are presented in Saeki (1991). We revisited those sites during the summer of 2008 and documented that the exclosures are intact and have not been compromised (with the exception that a door was ajar at Precipice and some browsing by deer within the exclosure had occurred). We were also successful in locating the associated control plots (with the exception of the Aunt Betty Pond exclosure). Thus we recommend that efforts to maintain these long-term benchmark sites be enhanced and that exclosures be periodically visited and repaired, as necessary. Additionally, all of the exclosure sites should be re-surveyed to provide valuable inferences regarding changes in deer browsing intensity since the last survey in 1988.

5). National parks are influenced by ecological, political, sociological, and economic considerations (Decker et al. 2001). A survey reported that managers in parks suggested that increasing public understanding of the management activities within parks, increasing public interest in park issues, understanding the range of public views, and the coordination of management activities with partners would assist in management (Leong

and Decker 2005). Further, under Director's orders (United States National Park Service 2003), the park service suggests public participation in the park planning process. We agree with these statements and suggest that increased efforts be directed at educating the seasonal and year-round residents of ANP, as well as tourists, about deer ecology and the associated management issues within the park.

6). We suggest that the park investigate methods for reducing vehicle collisions with deer via increased signage, education, by working with the communities, and by promoting the park and ride program currently in place.

7). The National Park Service management policies suggest cooperation between parks and other local and regional agencies (United States National Park Service 2000). We suggest collaboration with state agencies in monitoring and managing the deer population on ANP, and with educating the public.

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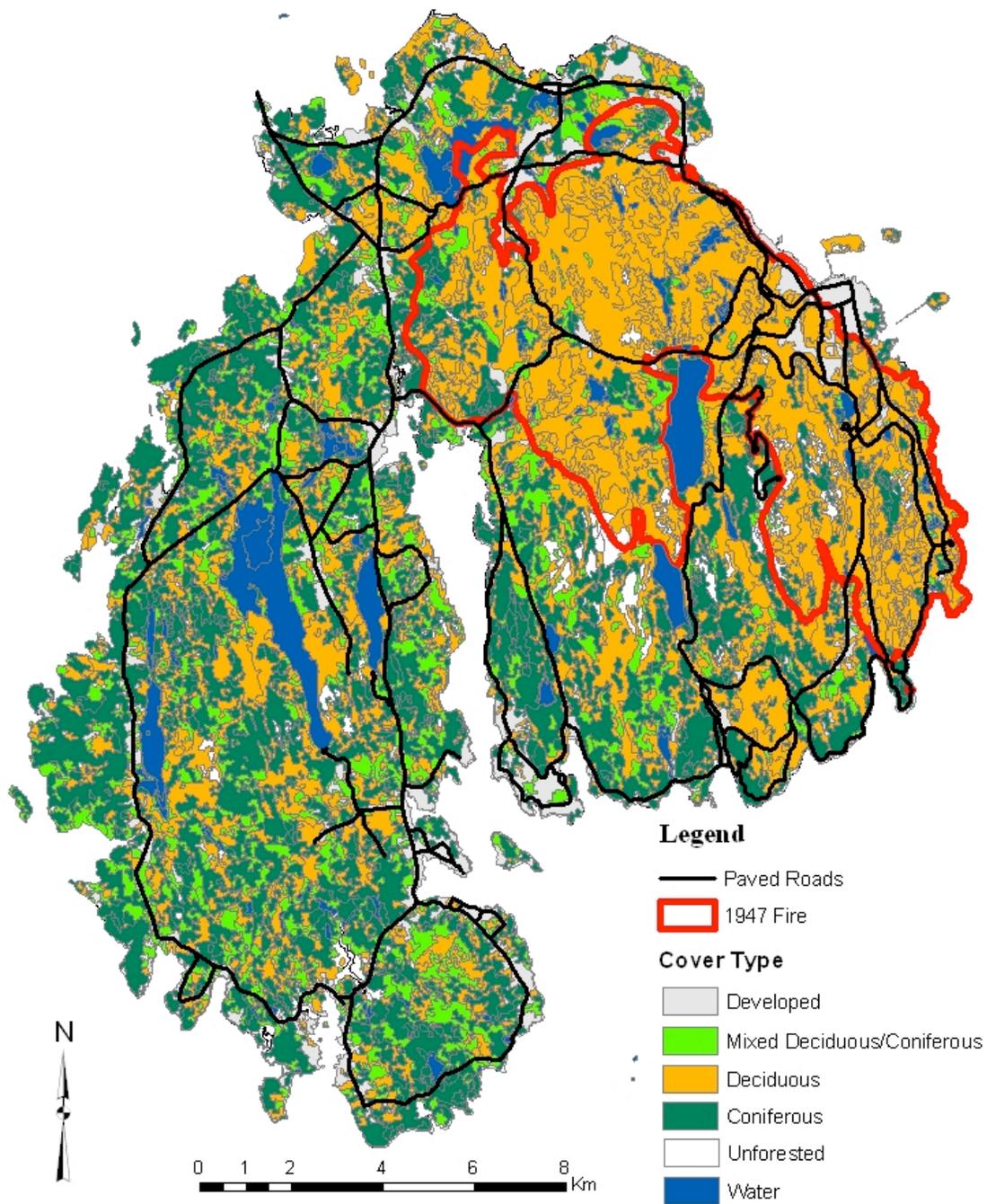


Figure 1. Composition of cover types on Mount Desert Island, Maine in relation to the fire of 1947.

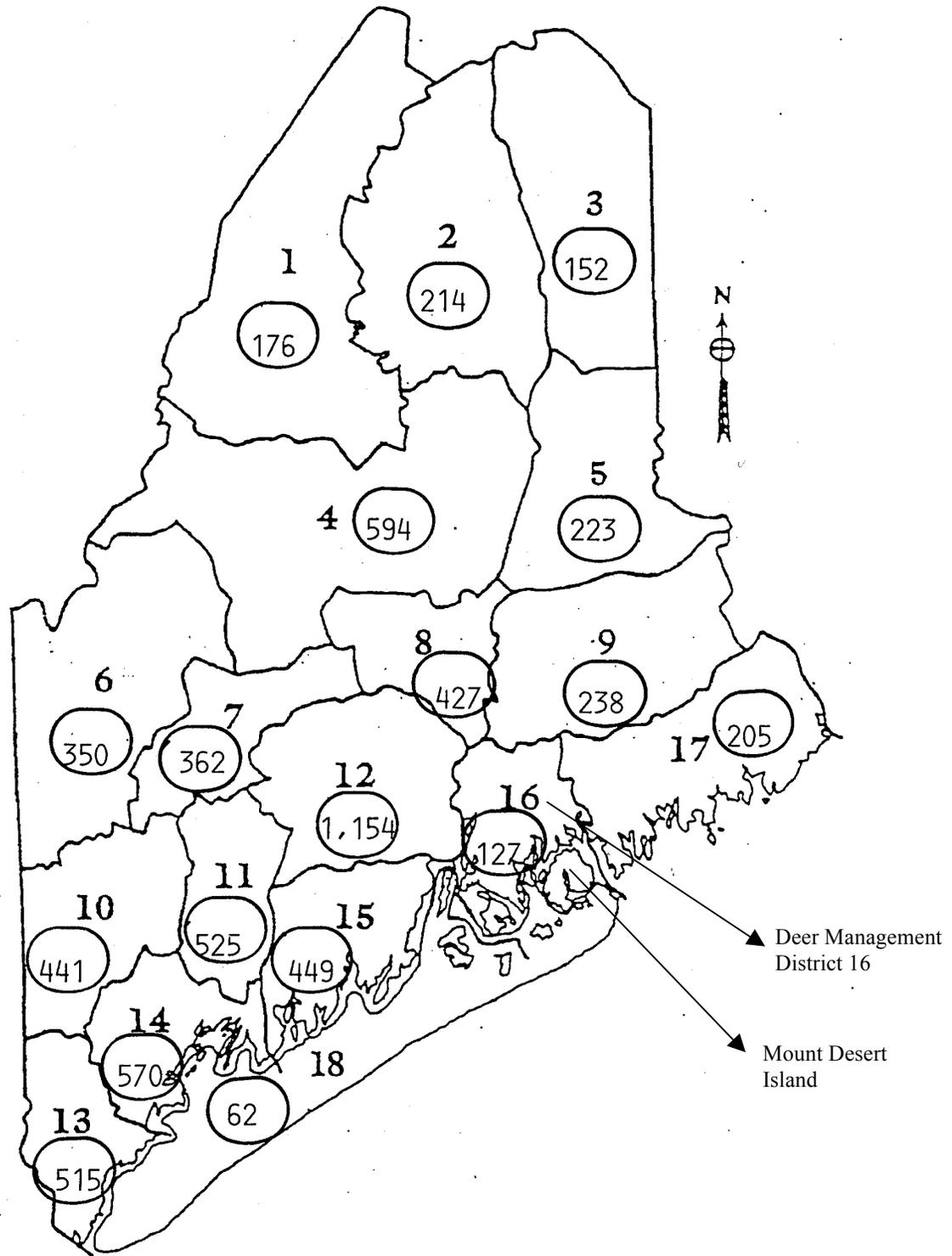


Figure 2. Deer management districts in Maine as sampled by the Maine Department of Inland Fisheries and Wildlife. Numbers in circles indicate the biological sample of the deer harvest in 1992.

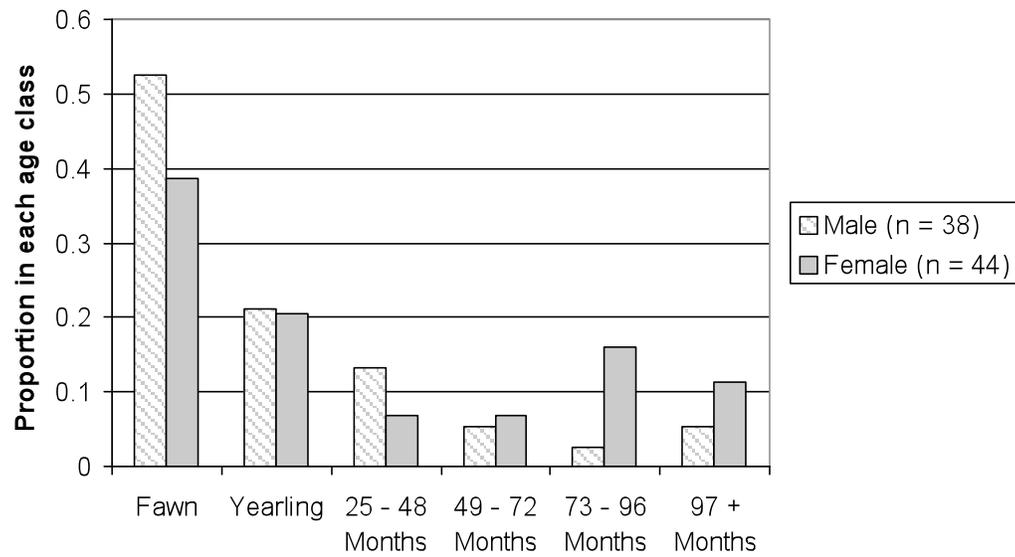


Figure 3. Age structure of radio collared and road killed white-tailed deer on Mount Desert Island, Maine, 1992 – 1994.

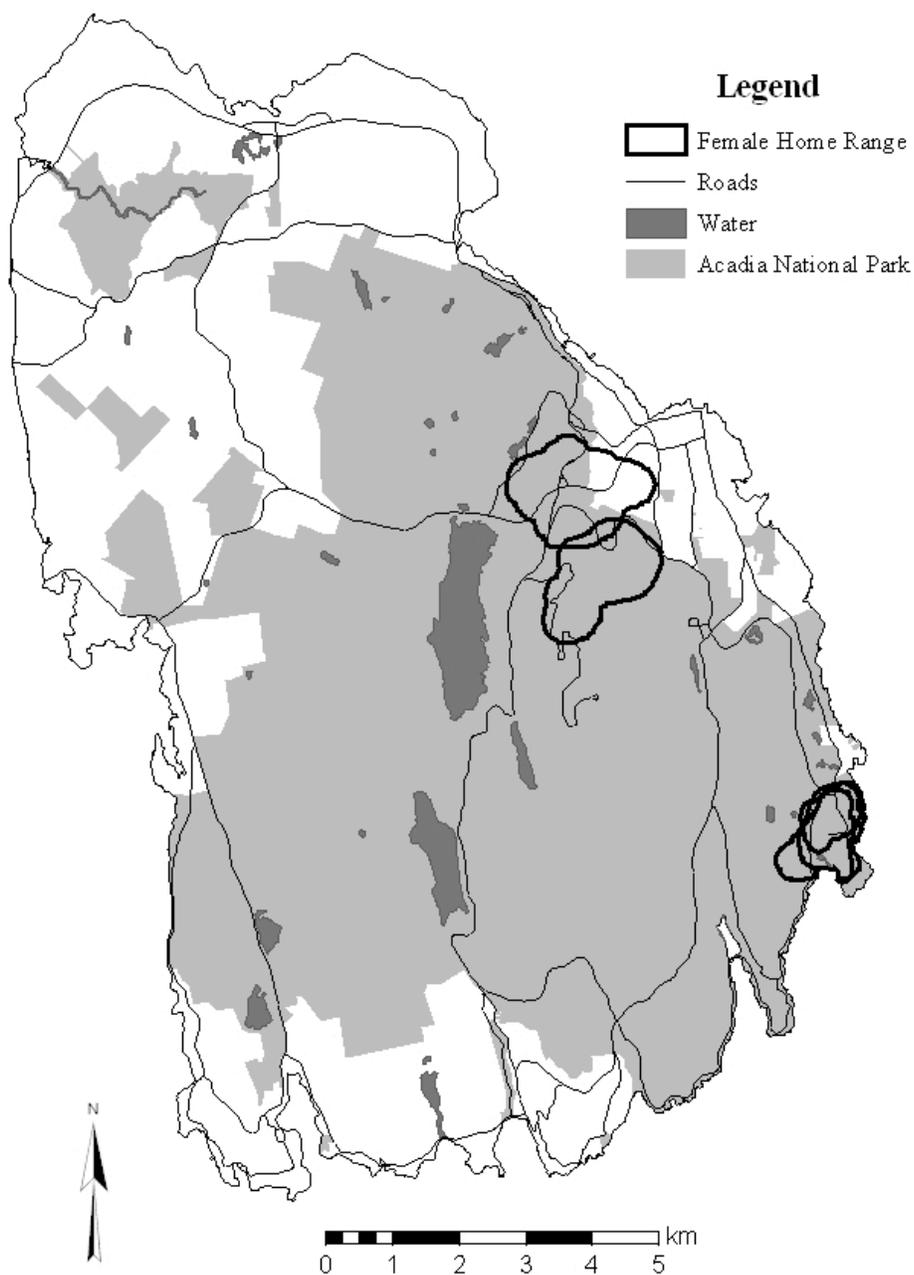


Figure 4. Home ranges (95% adaptive kernel) of female white-tailed deer during summer (n = 5), eastern portion of Mount Desert Island, Maine, 1992 – 1994.

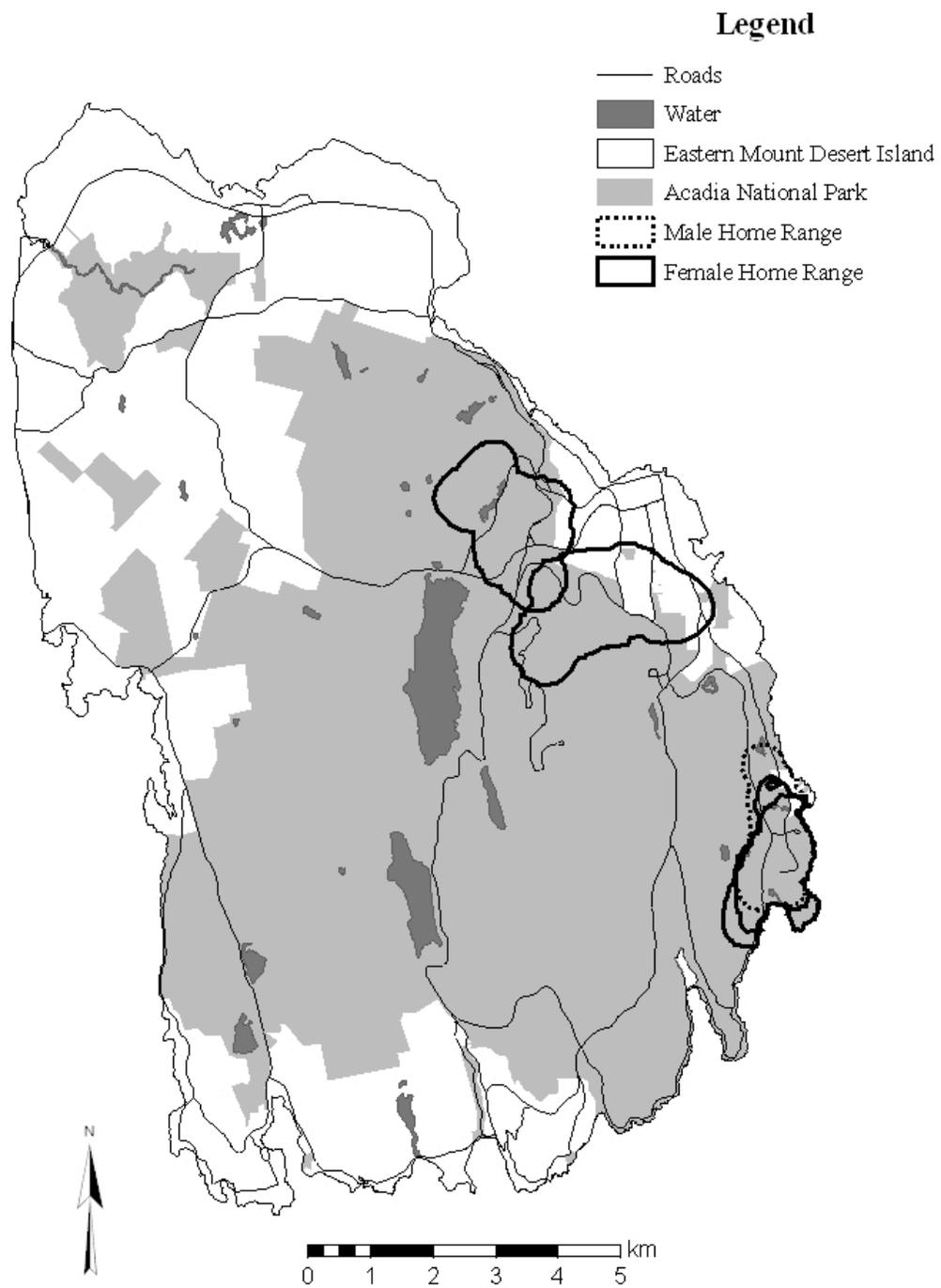


Figure 5. Home ranges (95% adaptive kernel) of male ($n = 1$) and female ($n = 4$) white-tailed deer during winter, eastern portion of Mount Desert Island, Maine, 1992 – 1994.

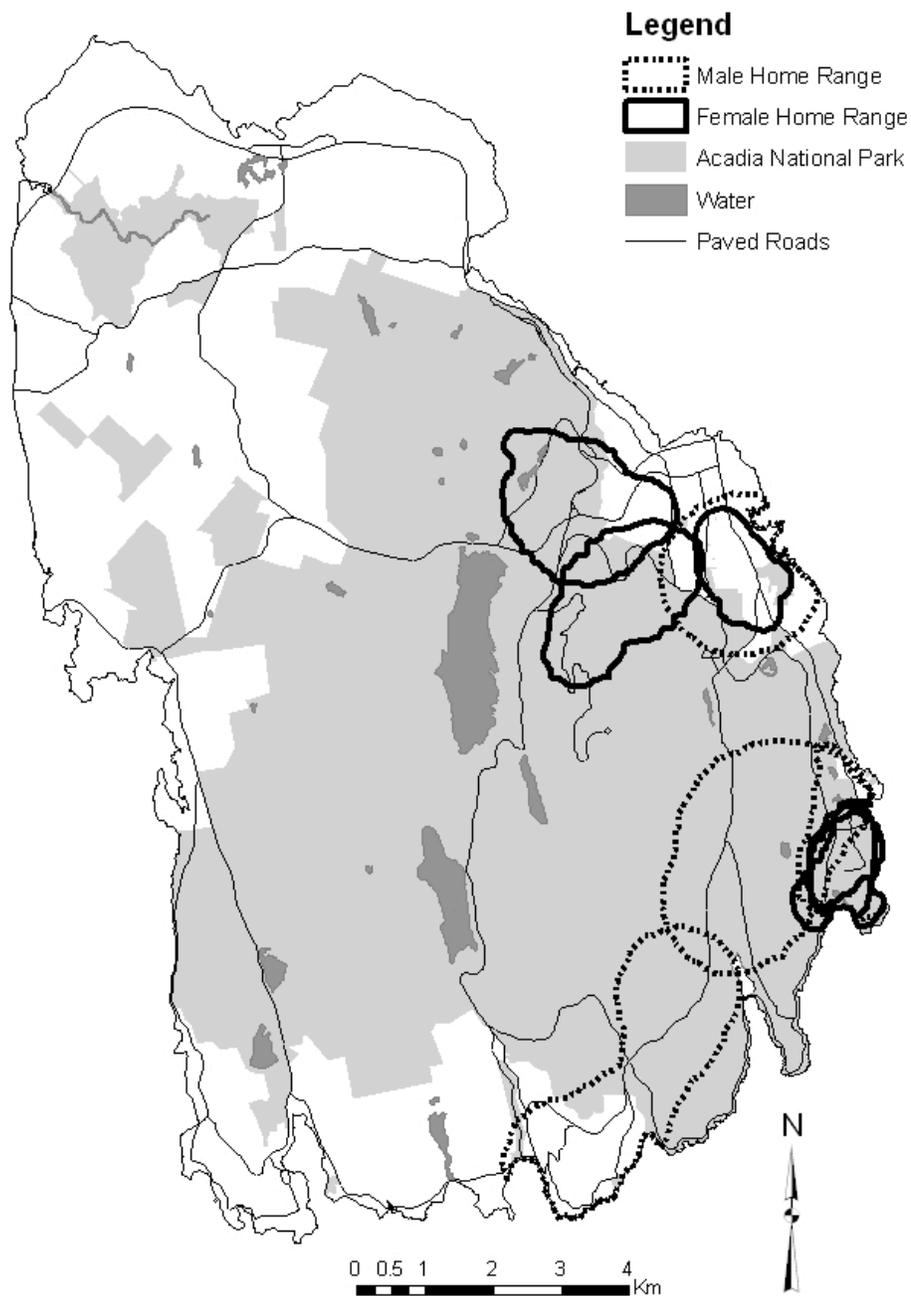


Figure 6. Yearly home ranges (95% adaptive kernel) of male ($n = 3$) and female ($n = 6$) white-tailed deer, on the eastern portion of Mount Desert Island, Maine, 1992 – 1994.

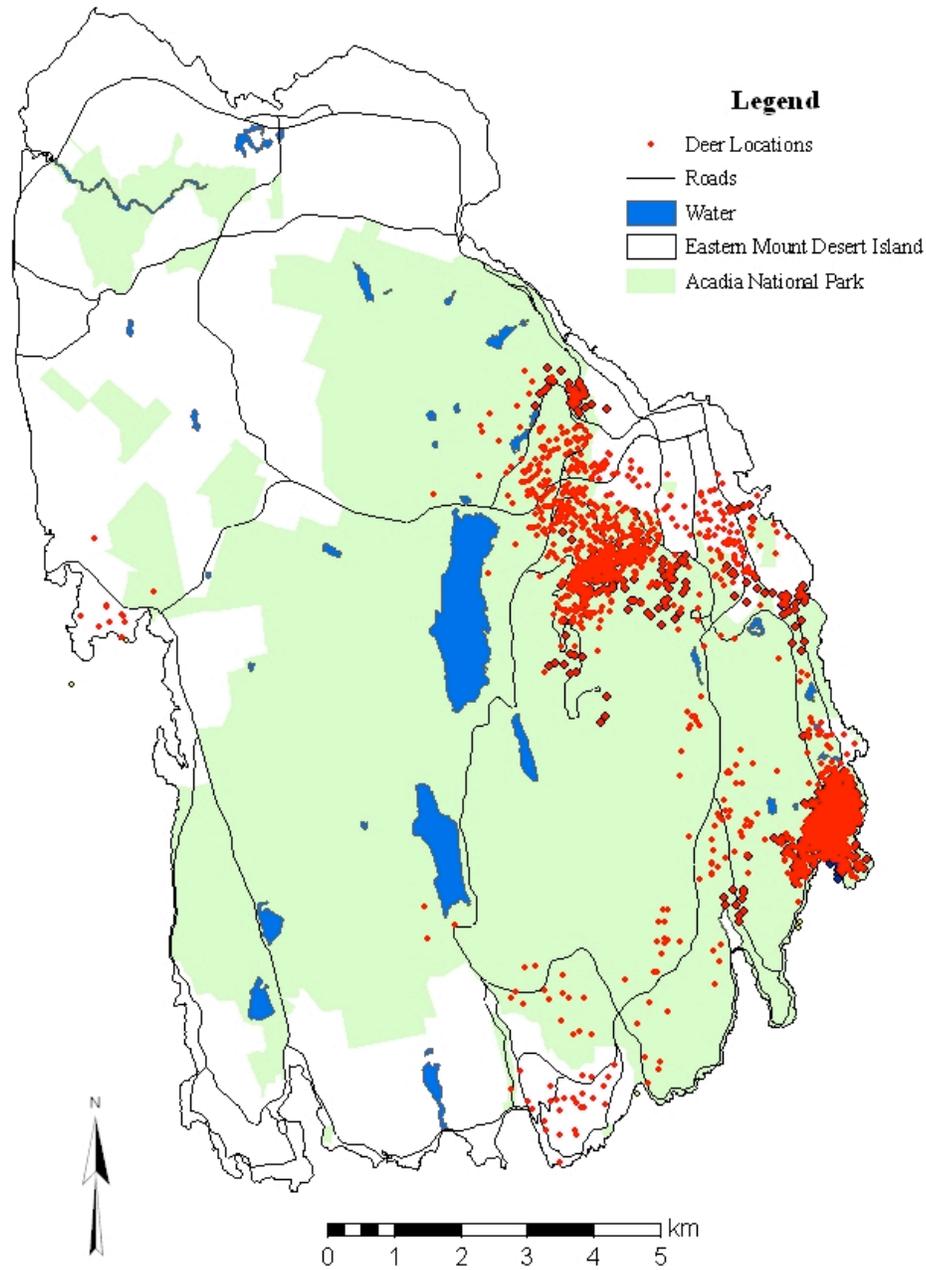


Figure 7. Radiolocations of white-tailed deer (1992 – 1994) in relation to Acadia National Park on the eastern portion of Mount Desert Island, Maine.

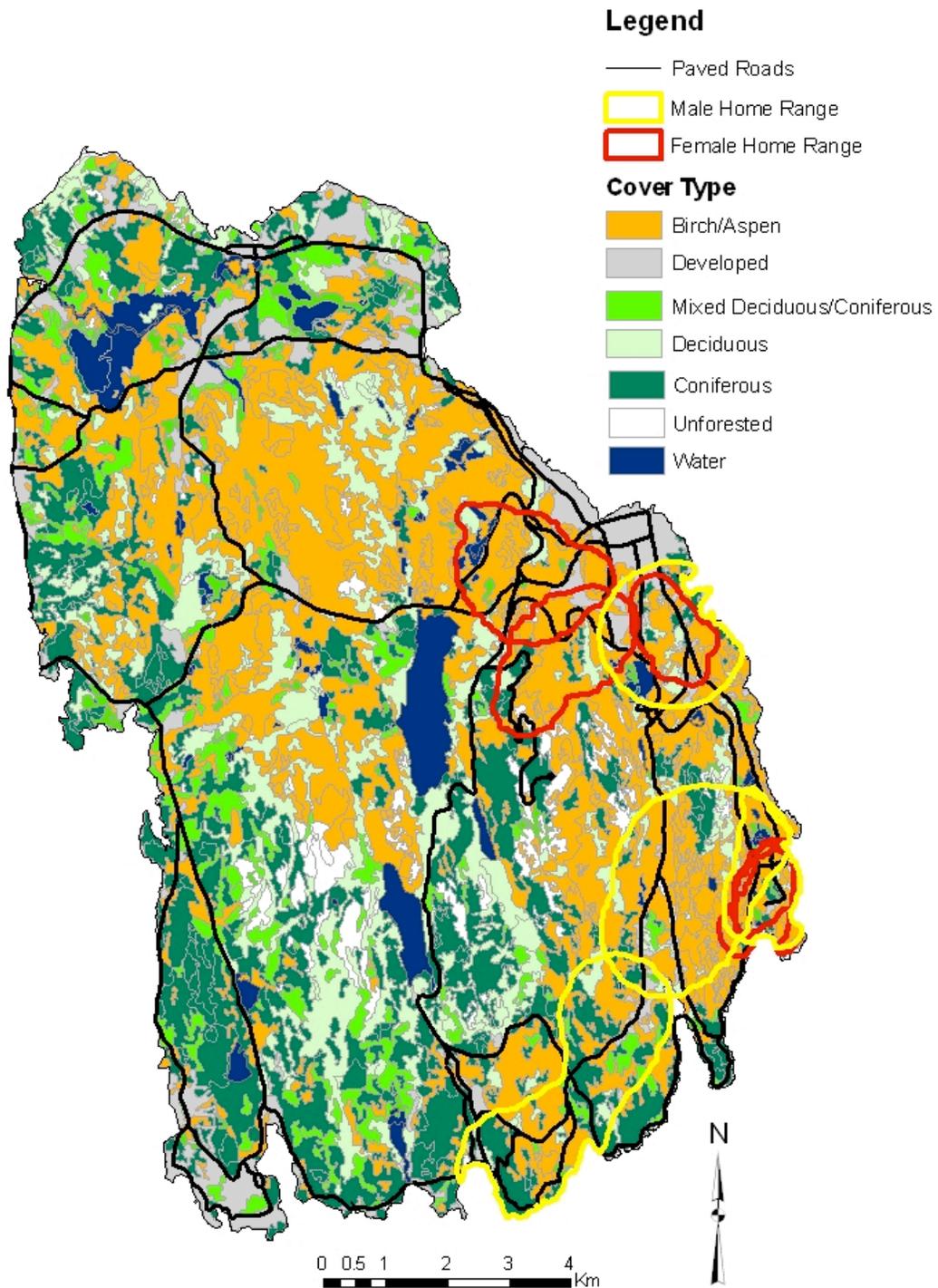


Figure 8. Yearly home ranges (95% adaptive kernel) of male (n = 3) and female (n = 6) white-tailed deer, eastern portion of Mount Desert Island, Maine, 1992 – 1994.

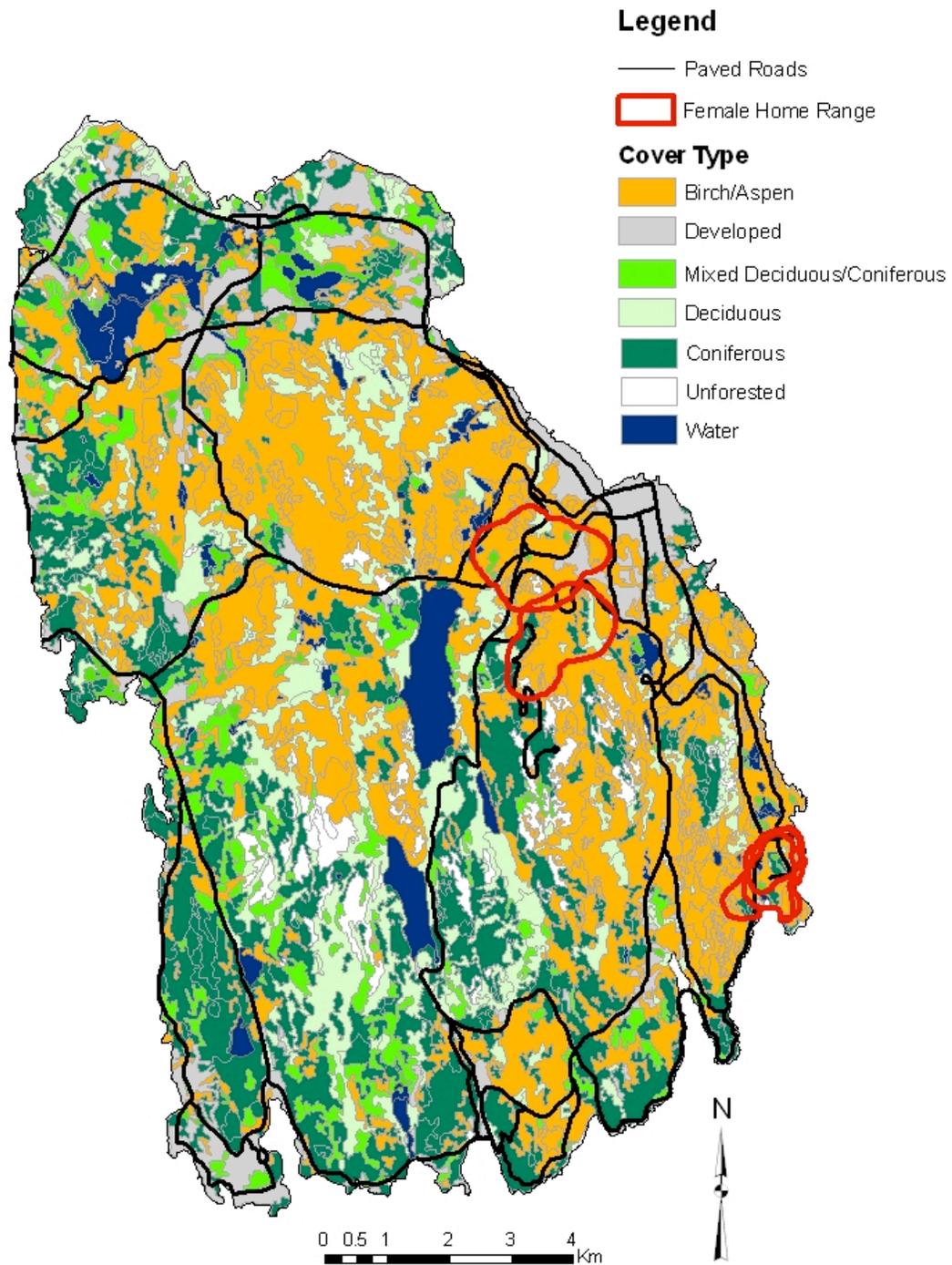


Figure 9. Summer home ranges (95% adaptive kernel) of female ($n = 5$) white-tailed deer, eastern portion of Mount Desert Island, Maine, 1992 – 1994.

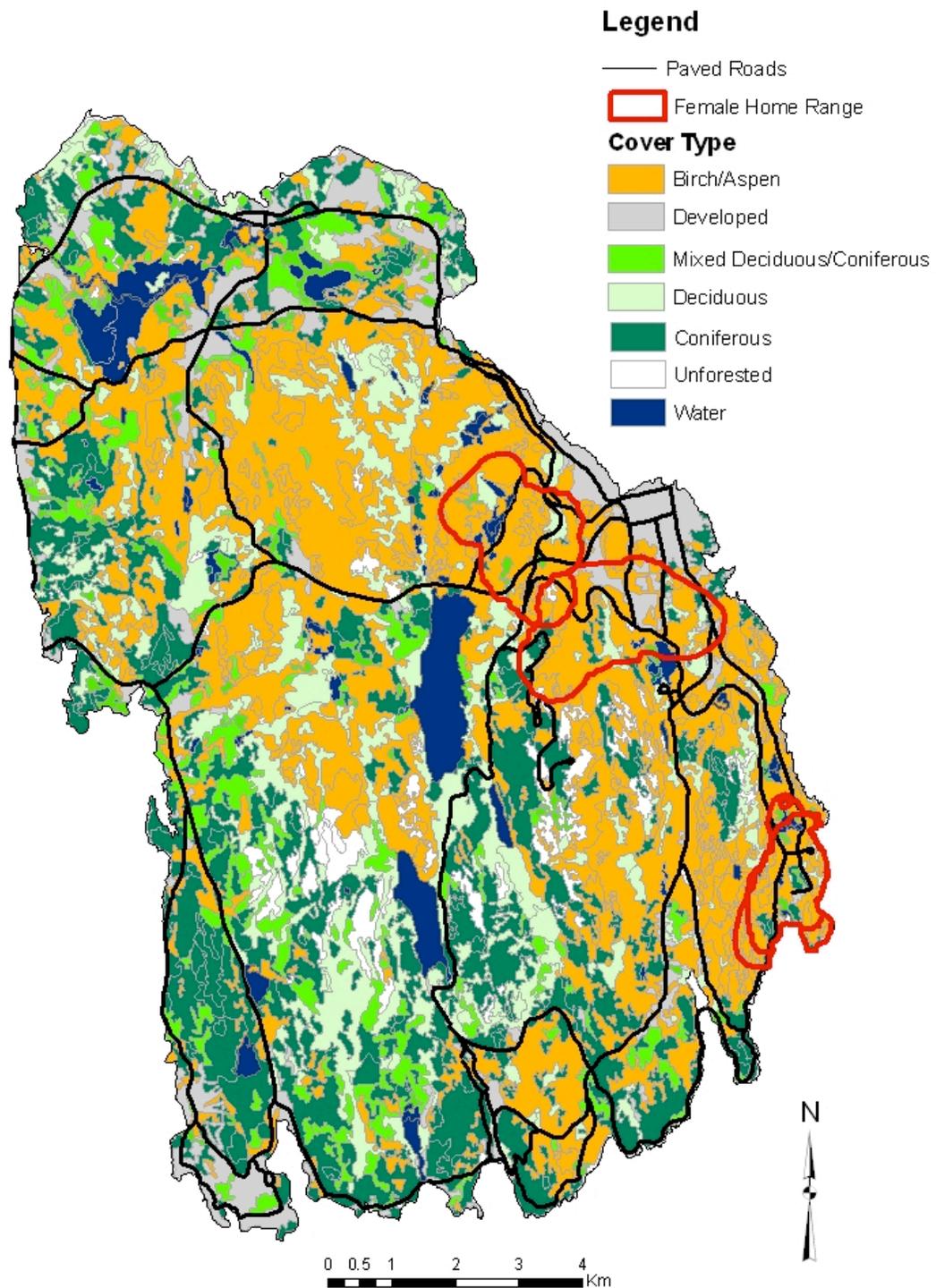


Figure 10. Winter home ranges (95% adaptive kernel) of female ($n = 4$) white-tailed deer, eastern portion of Mount Desert Island, Maine, 1992 – 1994.

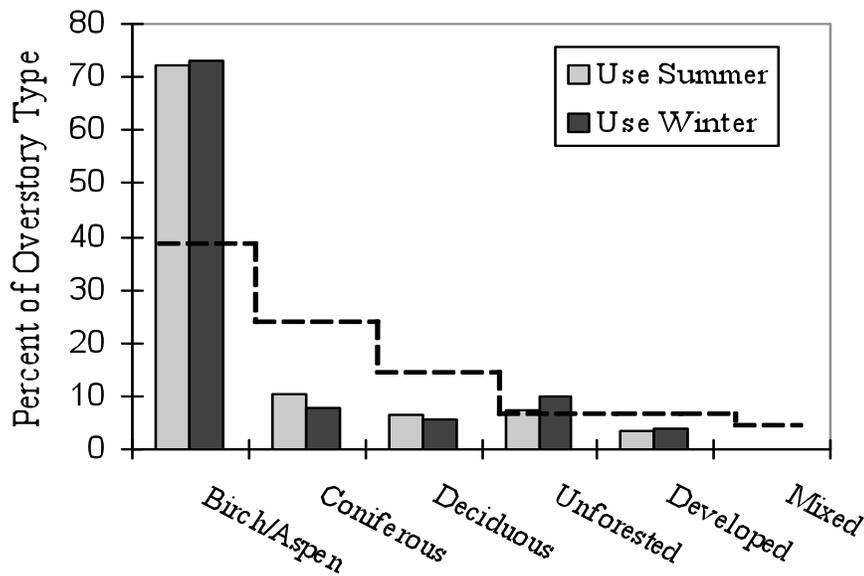


Figure 11. Seasonal variation in use of overstory types at the landscape-scale by female white-tailed deer on Mount Desert Island, Maine, 1992 – 1994. Use is the average percent of each overstory type within each deer home range. Dashed line indicates availability of each overstory type on the eastern portion of Mount Desert Island.

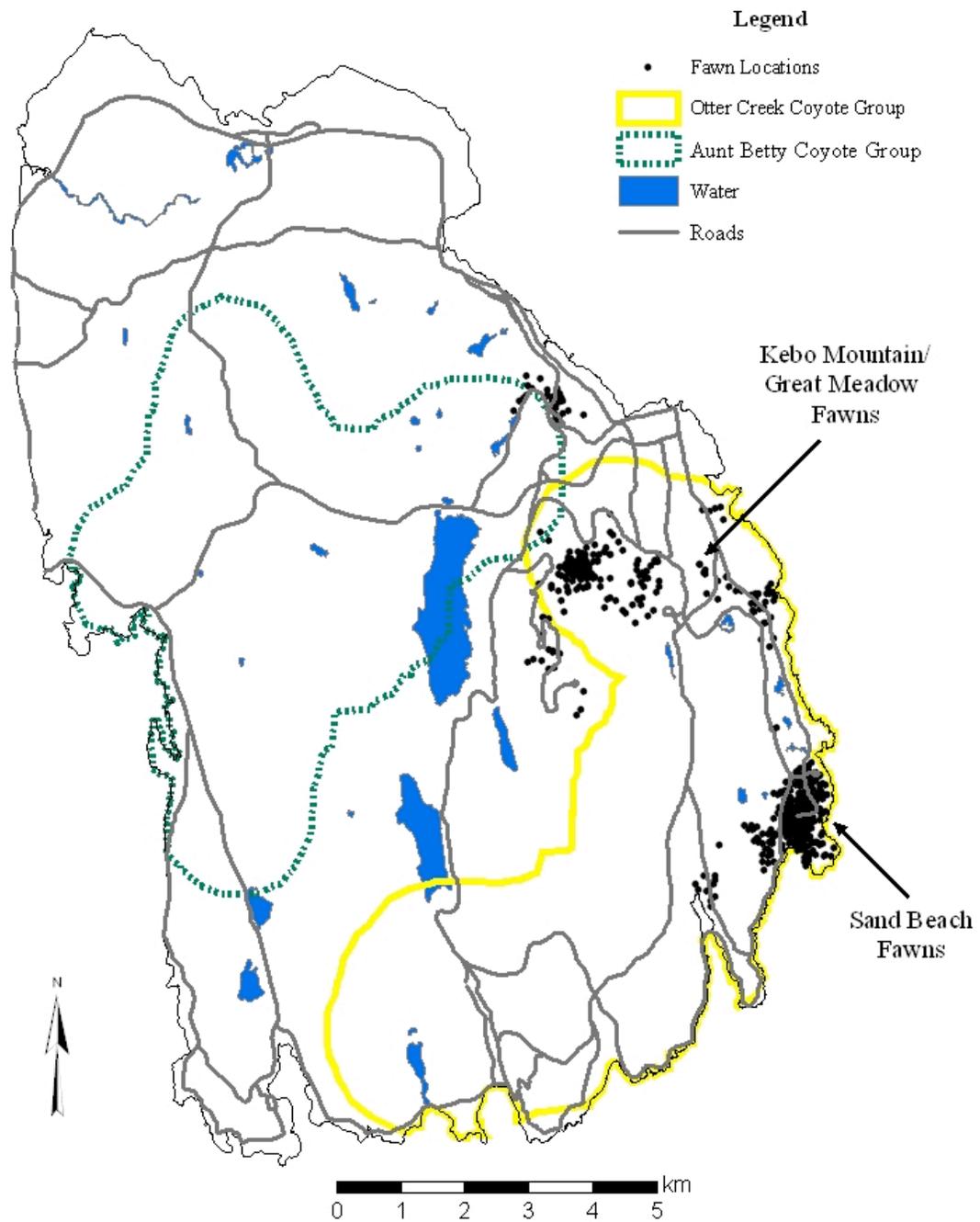


Figure 12. Radiolocations of white-tailed deer fawns (1992 – 1994) in relation to coyote home ranges (95% adaptive kernel), eastern portion of Mount Desert Island, Maine.

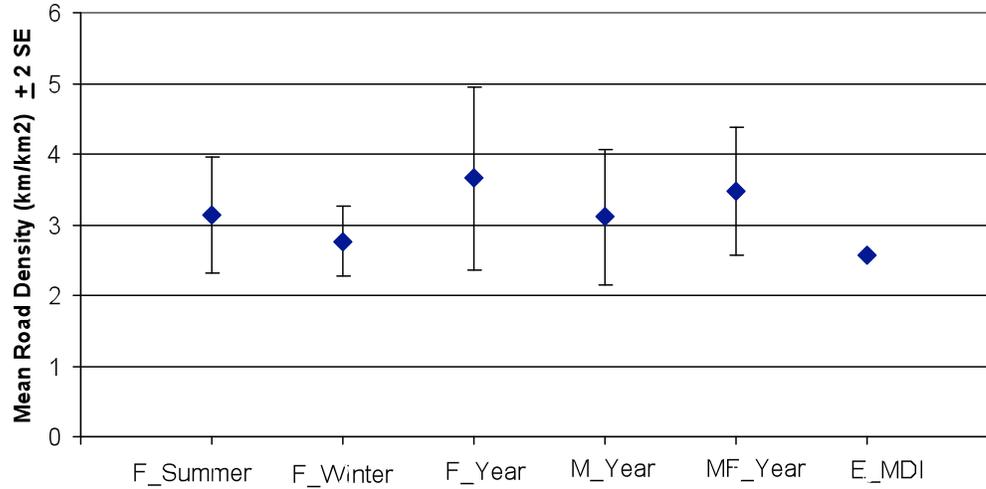


Figure 13. Density of roads within white-tailed deer home ranges (F_Summer [n = 5], F_Winter [n = 4], F_Year [n = 6], M_Year [n = 3], MF_Year [n = 9]) compared to the density of roads within the eastern portion of Mount Desert Island, Maine, 1992 – 1994.

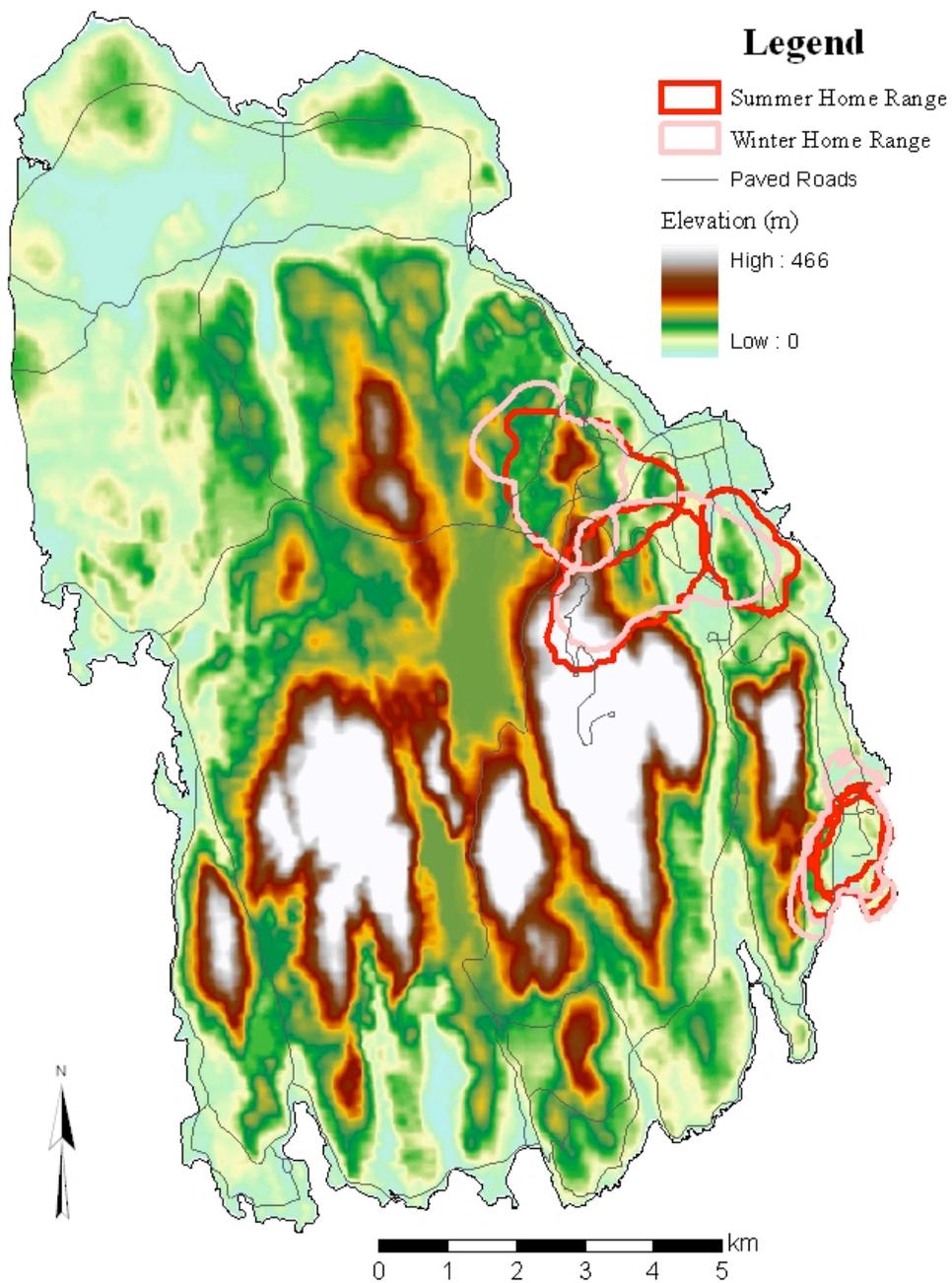


Figure 14. Elevation within female white-tailed deer home ranges (95% adaptive kernel) during summer (n = 5) and winter (n = 4), eastern portion of Mount Desert Island, Maine, 1992 – 1994.

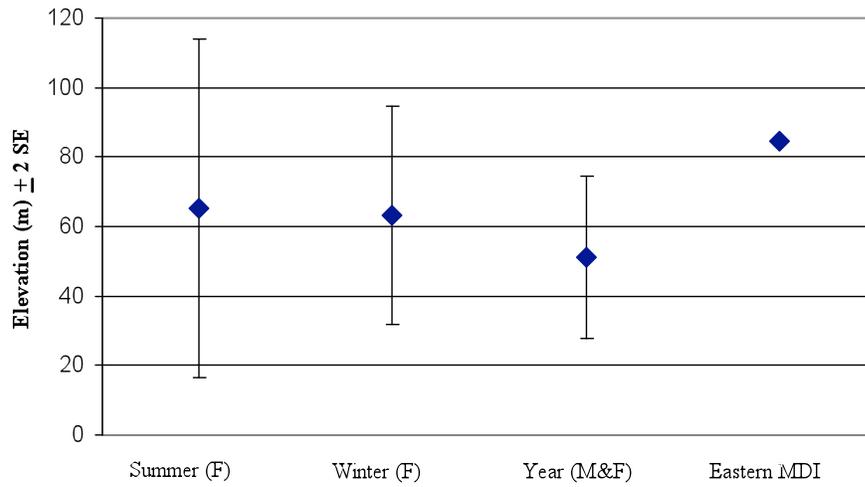


Figure 15. Mean elevation within white-tailed deer home ranges compared to mean elevation on the eastern portion of Mount Desert Island, Maine, 1992 – 1994.

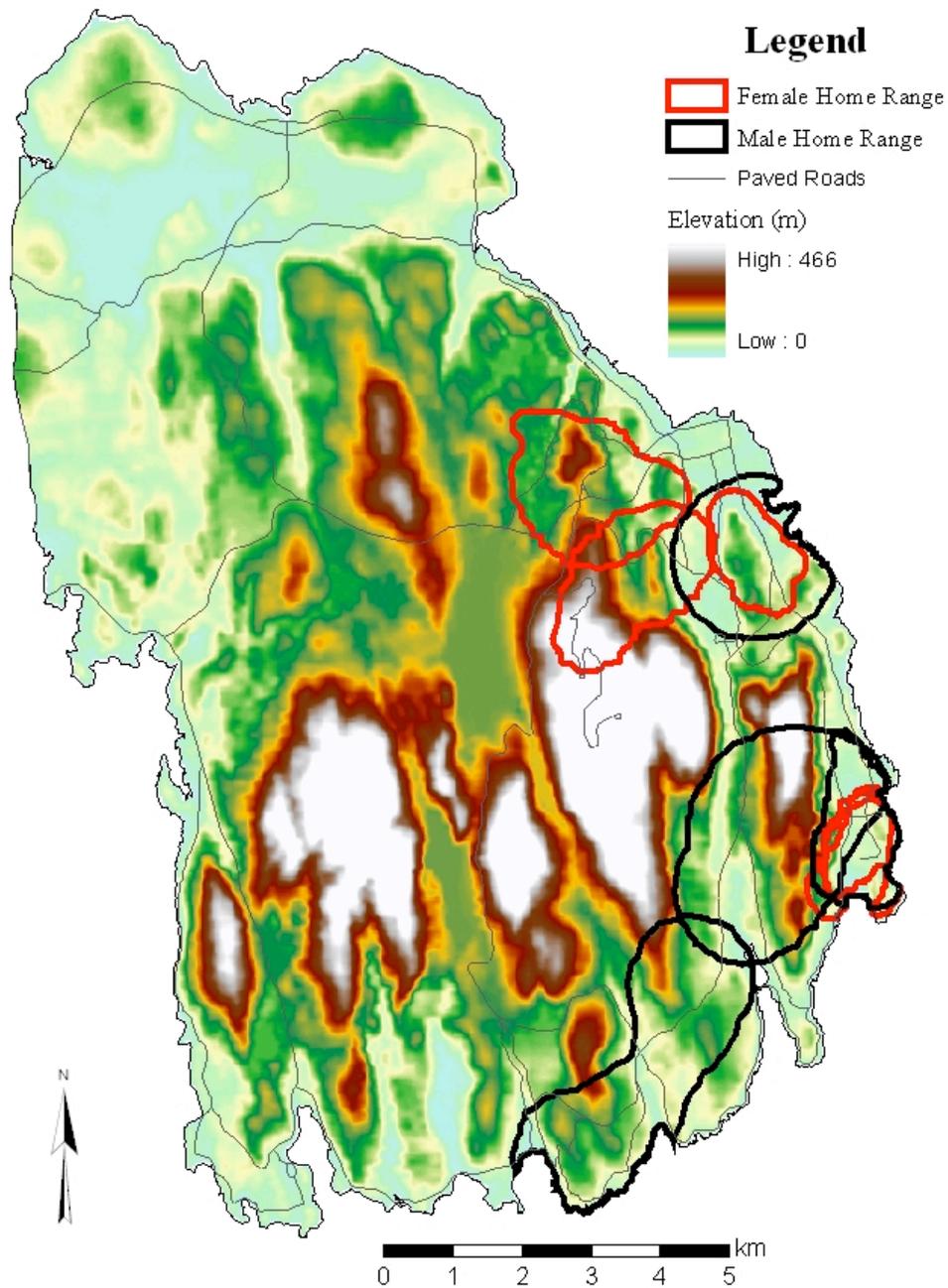


Figure 16. Elevation within male ($n = 3$) and female ($n = 6$) yearly white-tailed deer home ranges (95% adaptive kernel), eastern portion of Mount Desert Island, Maine, 1992 – 1994.

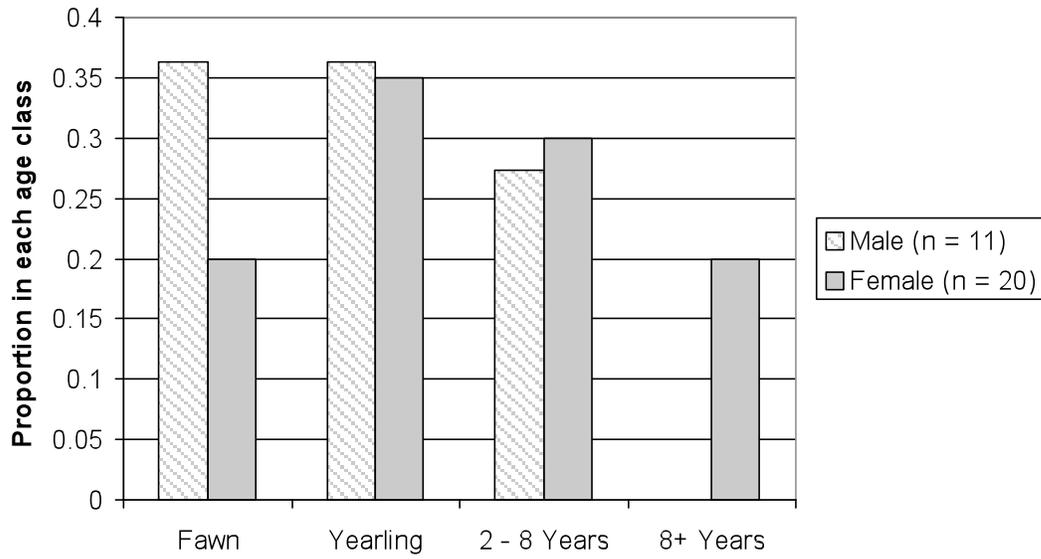


Figure 17. Age structure of road-killed deer on Mount Desert Island, Maine, 1991 – 1994.

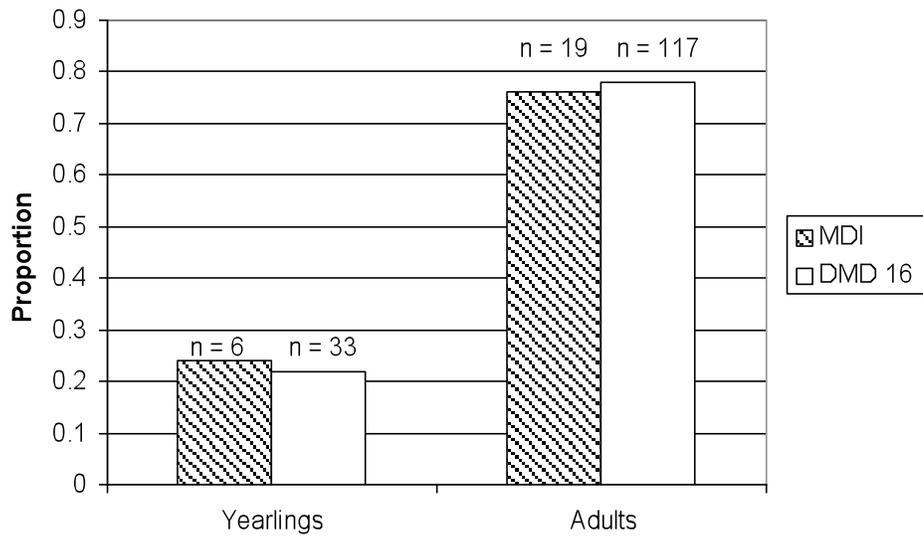


Figure 18. Proportion of yearling and adult does on Mount Desert Island (MDI) (1991 – 1994) and Deer Management District 16 (DMD 16) (1986 – 1993), Maine.