

EVALUATING IMPACT OF SELECTIVE HARVEST MANAGEMENT ON AGE
STRUCTURE AND SEX RATIO OF WHITE-TAILED DEER (*Odocoileus virginianus*)
IN ARKANSAS

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STRUCTURE AND SEX RATIO OF WHITE-TAILED DEER (*Odocoileus virginianus*)
IN ARKANSAS

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STUDY OBJECTIVES

The purpose of this research study was to address multiple issues relating to white-tailed deer management in Arkansas. I evaluated several white-tailed deer management questions that could be important to white-tailed deer managers. In this work, I combined age- and sex- structured stochastic population models with probabilistic models to evaluate the influence of demographic variation, environmental variation, and harvest regulations on white-tailed deer population dynamics. My research objective was to evaluate effects of regulatory actions at multiple spatial scales on white-tailed deer population dynamics. This objective was reached by addressing three primary goals:

- 1) Developed a white-tailed deer population model that incorporates demographic and environmental variation with regulatory actions to evaluate responses of white-tailed deer populations,
- 2) Developed a probabilistic modeling approach that provides the Arkansas Game and Fish Commission (AGFC) with an objective, scientifically rigorous, quantitative method for evaluating various white-tailed deer harvest management decisions, and,
- 3) Explored the effects of parameter uncertainty in the decision making process and apply these evaluations to assist in directing future research needs, data collection, and monitoring programs.

**CHAPTER I. SELECTIVE HARVEST PRACTICES, POPULATION
DYNAMICS, AND UNCERTAINTY IN WHITE-TAILED DEER
MANAGEMENT: AN INTRODUCTION**

INTRODUCTION

Few recreationally harvested mammalian species in the United States have been more intensively studied than white-tailed deer (*Odocoileus virginianus*). Active management by regulatory agencies is used to maintain deer populations at biologically and socially acceptable levels, while providing recreational opportunities for sportsmen (Woods et al. 1996). When making management decisions, the ability of regulatory agencies to accurately predict changes in population size and structure under different management programs is important.

Studies evaluating harvest management programs have focused on evaluating or inferring the relationship between harvest, population size, and population structure. The only information readily available to managers is harvest data (Carpenter 2000), which is a non-representative sample of the true population (Ditchkoff et al. 2000). Effectiveness of management practices cannot be inferred without population demographic data (e.g. abundance, survival, recruitment) (Lubow et al. 1996), but this information is lacking across the range of the white-tailed deer (McShea et al. 1997). Implementation of adaptive management for white-tailed deer has been called for (McShea et al. 1997, White and Bartmann 1997, Lancia et al. 2000), but little progress has been made. Thus, new techniques must be applied to white-tailed deer population management that allows managers to use available information to reach informed decisions. Population models

that allow for incorporation of available data, current knowledge, and explicitly account for parameter uncertainty can increase our ability to adequately manage white-tailed deer populations.

WHITE-TAILED DEER POPULATION MODELING

Because biological information on harvested deer is readily available (Carpenter 2000), a large number of white-tailed deer management techniques rely directly on harvest data (Roseberry and Woolf 1991, McCullough et al. 1990, Lubow et al. 1996). Hayne (1984) suggested that white-tailed deer managers could get better information on population trajectories through continued monitoring of indices (population size and habitat) rather than modeling populations based on demographic parameters. Hayne's (1984) concern with modeling approaches and recommendations regarding index values was that models must rely on simplified assumptions to remain practical. Recently, several authors (Anderson 2001, Thompson 2002) have discussed the pitfalls of using index values to monitor wildlife populations. Indices do not incorporate detection probability or measures of variability and are of limited usefulness for modeling population processes (Anderson 2001).

Roseberry and Woolf (1991) reviewed approaches that use deer harvest data to predict population dynamics. In order to compare these techniques, Roseberry and Woolf used the Crab Orchard National Wildlife Refuge (CONWR) herd as the "standard" to test each approach following suggestions by Downing (1977). In their review, methods based on catch per unit effort (variant D) and reconstruction methods (variant B: Downing 1980) were rated good, while all other methods were rated either poor, fair, or were unrated. However, methods of population reconstruction (see Population Size) are

unreliable and have underlying assumptions that are difficult to meet (Williams et al. 2002). Catch per-unit effort methods rely on the assumption that the ratio of the number of animals caught (harvested) per unit effort is proportional to their number in the population, and depend on accurate estimates of effort, harvest mortality, and large sample sizes (Novak et al. 1991). Few methods discussed in Roseberry and Woolf incorporated population demographic rates, which are necessary for accurate population management (Lubow et al. 1996, White 2000).

Several state agencies have used sex-age-kill (SAK) methods of population analysis (Eberhardt 1960, Creed et al. 1984). SAK models are retrospective approaches (Hansen 1998, Williams et al. 2002), which have several underlying assumptions regarding parameter estimates and the mechanistic relationships between harvest data and population processes. SAK model parameters use index values estimated from harvest data, therefore the usefulness of SAK models is limited to being a coarse evaluator of population size (Williams et al. 2002).

Walters and Gross (1975) evaluated the effectiveness of simulation modeling to develop decision-making criteria and assist with management planning. They found that simulation modeling provided managers with opportunities to explore “what-if” scenarios for alternative management objectives. Using a simulation modeling approach, Bender and Roloff (1996) assessed strategies for increasing trophy buck production and found that increasing the proportion of bucks in the population resulted in lower harvests, with increased buck age structure. Bender and Roloff’s (1996) simulations also suggested that systems which restrict harvest of young age-class deer did not result in increased trophy animals.

McCullough et al.'s (1990) linked sex harvest strategy (LSHS) was developed to allow managers to evaluate and plan management strategies strictly based on harvest data. McCullough's model was based on the "black box" concept, which assumes that "a deer population is a far more effective integrator of variables than the population researchers are (McCullough 1984)." Lubow et al. (1996) simulated 2 deterministic population models and found the LSHS approach was inadequate, further stating that reliable information on population demographic rates was needed to reach optimum harvests.

Xie et al. (1999) constructed a deer population model to evaluate responses to management options (primarily related to changes in harvest rates). Through simulation modeling, Xie et al. (1999) determined that optimal deer management objectives in Michigan (defined in terms of population size and % antlered bucks in the population) were reached under harvest rates of 20%. Using these harvest rates, the model of Xie et al. (1999) reached the quantity goal (372,500) and nearly reached the quality goal (35% antlered bucks). Concerns with the model applied by Xie et al. (1999) include, (1) harvest rates for male and female segments were varied in 10% and 5% intervals, respectively (which defined 35 harvest scenarios), (2) no incorporation of demographic variation in vital rate parameters, (3) fawn sex ratios (based on female age) were constant for each model run and in no case were fawn sex ratio's female biased, (4) input age structure distributions and sex ratio were based on information collected from harvested individuals, which is inherently biased, and (5) harvest rates of 20% would be considered low by most managers.

To evaluate the hypothesis that maximum sustained yield was compatible with trophy management Jenks et al. (2002) modeled population response to harvest using harvest data, vehicle-kill data, and population size estimates. Results from Jenks et al. (2002) indicated that percentage of trophy males (as defined by McCullough 1984) declined over time as yearling harvest increased. The modeling approach of Jenks et al. (2002) used initial population sex ratios near unity, constant recruitment rates over time, and assumed that changes in age and sex composition of the population was indexed by changes in the harvest, e.g. no hunter selectivity.

One common theme from previous deer population modeling approaches is that in a majority of scenarios deterministic models were used, with population parameter indices constructed using harvest data, and vital rates were constant throughout the modeling procedures. When constructing or implementing white-tailed deer management programs, managers need the ability to integrate and evaluate multiple management scenarios while incorporating variation in population processes and uncertainty to make scientifically sound management decisions.

POPULATION PARAMETER RELATIONSHIPS

The structure (age and sex distribution) of wildlife populations exhibits considerable variation over time. Fluctuating dynamics in white-tailed deer populations are caused by variation in individual vital rates. Using stochastic population models (Lande et al. 2003, Phillips and White 2003); managers have the ability to model fluctuating dynamics by linking population processes and vital rates. With stochastic population models, managers can evaluate the intricate connections between

demographic and environmental processes, and resulting influence on population dynamics.

Due to the economic significance of white-tailed deer, there have been multiple research studies evaluating population relationships between survival, recruitment, harvest, and abundance. However, knowledge of population parameter relationships does not exist across broad temporal and spatial scales, thus exact knowledge of population vital rates is limited across the range of white-tailed deer. From a management perspective, factors of interest to managers are population age structure, population sex ratio, abundance, and age-sex specific mortality rates, all of which are typically lacking when constructing and evaluating white-tailed deer management plans. Below I provide primary vital characteristics that are expected to influence white-tailed deer population dynamics, and I review the current state of knowledge regarding these vital rate parameters.

Sex Ratio

In their classic paper on sex ratios, Trivers and Willard (1973) hypothesized that females in poor condition should produce daughters rather than sons. Trivers and Willard (1973) hypothesized that weak females born to mothers in poorer condition are expected to have higher reproductive potential than weak males. However, this relationship is not consistent with patterns found in white-tailed deer (Verme 1985). In a classic review for evidence of sex ratio variation across a broad range of mammals, Clutton-Brock and Iason (1986) found that *Odocoileus* sex ratio's declined with maternal age, and increased when individuals were subjected to nutritional, habitat quality, or population density stressors (Clutton-Brock and Iason 1986, pp. 364.)

One suspected cause of variation in fetal sex ratio in white-tailed deer is nutritional restriction due to conditions affecting habitat quality and quantity. McCullough (1979) noted that production of female progeny was more likely after periods of reduced population size, leading to increased available habitat. However, Verme (1983) attributed skewed sex ratios to the age classes present and those classes predominance in producing males. Verme (1965, 1967, 1969, 1985) found that females at lower nutritional level were more likely to have male over female fawns. Verme (1967) also showed that when nutritional conditions were moderate, fawn sex ratios were near unity. Wilson and Sealander (1971) estimated a fetal sex ratio of 42:58 (41% males) across Arkansas and concluded no statistical differences from unity between regions and statewide. Verme's (1983) review of sex ratios in *Odocoileus* exhibited several interesting results mainly that the progeny sex ratio (expressed as % males) declined in *Odocoileus* as gross fecundity, age, and litter size increased. Verme's (1983) discussion of declining male progeny concurs with earlier statements by Trivers and Willard (1973) that "...decreased maternal investment per offspring (maternal parity and litter size) is correlated with reduced sex ratios at birth". Conclusions from Verme (1983) indicate that fawn sex ratio's were closely linked to female nutritional status. Verme (1985) determined that yearling does on restricted diets produced fewer male offspring (22%) as compared to yearling does on non-restricted diets (48% males), which he attributed to yearling females mimicking 2.5 year old does based on results from Ozoga and Verme (1986b). However prime age (2.5-7.5) females produced 71% males on restricted diets, compared to 49% males on non-restricted diets, while old does (>8.5 years) produced fawns in unity (Verme 1985). Using necropsy data, Folk and Klimstra (1991) found a

relatively high ratio (74%) of male fetuses for Key deer (*Odocoileus virginianus clavium*) over a 21-year period, which was partially attributed to food supply limits.

Another possible mechanism causing fetal sex ratio variation is female age at breeding. Verme (1967) estimated fawn sex ratios near unity (43.9% and 50.9%, respectively) for 2-year old and prime age does, while sex ratio for yearlings was 31% males. Richter and Labisky (1985) found that females >5 years old produced ~32% male fetuses, and that overall fetal sex ratios were skewed towards males on hunted sites, but towards females on non-hunted sites, where older population age structure would be expected (Ditchkoff et al. 2000). Prior breeding success has been shown to influence fawn sex ratios by Ozoga and Verme (1986a) as females that produced fawns in one year had a lower proportion of male progeny in the following year.

Caley and Nudds (1987) provide one possible explanation for sex ratio variation due to nutritional limitations. The hypothesis of local resource competition (Clark 1978) between mothers and offspring for limited resources in the mother's home range could influence offspring sex ratios. White-tailed deer are a matriarchal species, of which female offspring tend to establish home ranges that over-lap the mother's (Campbell 2003), while male offspring tend to disperse from the natal range (Verme 1983). Caley and Nudds (1987) stated that, "...local resource competition between does and daughters could increase cost to the females to the point that, despite the potentially greater costs of male offspring before weaning, males become cheaper to produce (Caley and Nudds 1987, pp. 455)." Therefore, because female fawns tend to congregate around their natal area (Campbell 2003) while males tend to disperse, maternal investment may be higher for female than male fawns (Demarais et al. 2000).

The impact of adult sex ratio on population productivity is less understood. While managers expect that shifting population sex ratio can influence population productivity, few experimental studies have been conducted to evaluate the impacts of population sex ratio on breeding success. Hayne (1984) goes so far as to state “Except that the adult sex ratio of a white-tailed deer population indicated whether mortality has been higher for one sex than for another, it is not a very useful management tool (Hayne 1984, pp 208).” Verme and Ozoga (1981) determined that as time between the onset of estrus and insemination increased, fawn sex ratios skewed more towards males (13-24 hours: 14% males; 49-96 hours: 80% males). Jacobson (1992) hypothesized that increased adult male:female ratios caused the breeding peak to shift 3 weeks based on data collected from harvested individuals. Relating Jacobson (1992) to Verme and Ozoga (1981), this could lead to increased breeding synchrony shifting fetal sex ratio towards females. However, as stated by White et al. (2001), results from Jacobson (1992) could be confounded with improved herd condition caused by reductions in density over the study period. White et al. (2001) evaluated effects of adult sex ratio on productivity of elk and mule deer, and concluded that post-harvest sex ratios had little impact on population productivity. Peterson et al. (2003), through simulation modeling, concluded that while fetal sex ratio are often ignored in population modeling, management studies should address fetal sex ratios when resources are limited.

Reproduction and Recruitment

Estimates of reproduction and recruitment are essential for understanding and management of white-tailed deer populations (McCullough 1979, Rhodes et al. 1985). Recruitment of white-tailed deer may be influenced by many factors, including; 1)

density dependent and density independent processes, 2) female nutritional levels, and 3) female breeding age.

McCullough (1979) documented reduced fawn recruitment at high densities of enclosed white-tailed deer on the George Reserve. In South Carolina, Rhodes et al. (1985) found that fetal number was significantly affected by female breeding age (No. of fetuses increased with female age), and that twinning occurring more frequently in older individuals. Rhodes et al. (1985) estimated mean fetuses/pregnant female for 4 age classes (fawn=1.06, yearlings=1.56, sub-adults=1.73, adults=1.76; Table 1, pp 383). Verme (1967) evaluated reproduction of females across three age classes (yearlings, 2-year olds, and prime age) under different nutritional regimes and found mean fawn production (fawns/doe) was 0.54, 1.43, and 1.50 across age classes.

Folk and Klimstra (1991) hypothesized that low levels of reproductive performance of Key deer were nutritionally driven. Based on necropsy data from Folk and Klimstra (1991 Table 2, pp. 389), mean fetuses/pregnant female (across age classes) was 1.17, where 54% of the total females examined were either pregnant or lactating. Estimated reproductive performance of white-tailed deer in Arkansas taken from individuals harvested during hunting season, highways kills, or spotlighting harvest ranged regionally from 1.63 fetuses/doe to 1.76 fetuses/doe (1.66 fetuses/doe across Arkansas) with a high pregnancy rate (Wilson and Sealander 1971). In Mississippi, Jacobson (1992) estimated reproductive performance for females > 2.5 years old as varying between 1 and 2.20 fetuses/female under restricted buck harvest and increased doe harvest regimes. Based on currently available estimates, across the range of white-

tailed deer, average fetus counts are relatively consistent, typically < 1 for fawn age classes, while varying from 1-2 for older females.

Age Structure

Across the United States there is little information available on the population age structure of white-tailed deer and available estimates are badly biased (Osborne et al. 1992, Trenkel et al. 2000). The only age-specific information gathered by managers is from harvested white-tailed deer, which is an unrepresentative sample of the true population. Tooth wear and replacement techniques are the standard for aging white-tailed deer (Severinghaus 1949). Severinghaus's (1949) approach has raised concerns regarding its accuracy due to limited sample size (Gee et al. 2002). In certain situations, studies evaluating fawn recruitment rates, fetal sex ratios, or fetal growth rates can provide ancillary information regarding the true population age structure of the female segment of the population (S. Ditchkoff, Auburn University, personal communication). This type of non-selective harvest can provide managers with estimates of the true age structure of the underlying population; however this information is typically only taken from females, and is not widely available.

Population Size

As Seber (1982) states "As a first step in understanding the structure and dynamics of a natural population it is essential to know something about the population size and related parameters such as the birth- and death-rates, etc. at given points in time (Seber 1982, pp. 1)." Hayne (1984) offers the view that knowledge of white-tailed deer population size was overestimated as a tool for managers, and more importance should be given to estimates of relative abundance and population trajectories. Hayne's (1984)

opinion was that index values of population abundance could provide adequate management information. Detecting a change in population size that requires some management action necessitates considerable effort (Thompson et al. 1998). Thus, approaches using relative abundance for management planning are limited in usefulness. Seber (1982) and Williams et al. (2001) provide a comprehensive list of techniques and statistical approaches for estimating population size.

Historically, several techniques have been used to estimate ungulate population sizes, including pellet counts (Fuller 1991, 1992), drive counts (McCullough 1979), night spotlighting (McCullough 1982), complete census (McCullough 1979), aerial surveys (Trenkel et al. 1997, Cogan and Diefenbach 1998, Samuel et al. 1992, Steinhorts and Samuel 1989), and population reconstruction (Fry 1949, McCullough 1979, McCullough 1990, Roseberry and Woolf 1991, Osborne et al. 1992).

Several authors have evaluated and applied the above techniques for estimating white-tailed deer abundance. Fuller (1991) evaluated use of pellet counts (Taylor and Williams 1956, Batcheler 1975) to index white-tailed deer population status by comparing pellet count estimates with results from an aerial survey and a demographic model from an intensive study of white-tailed deer in Minnesota (Fuller 1990). Results from Fuller (1991) indicated that pellet counts “probably do not unambiguously reflect deer abundance” (Fuller 1991, pp. 395, but see White 1992, Fuller 1992).

Fryxell et al. (1991) applied cohort analysis to evaluate temporal variation in harvest and recruitment in an Ontario white-tailed deer population. While their analysis showed two distinct population changes, comparisons to the underlying population were based on reconstruction methods using constant survival rates and on correlations

between indices. Fryxell et al. (1991) concluded that frequent changes in management practices to reverse short-term trends in harvest success or population size may cause greater fluctuations in abundance than a constant harvesting policy.

McCullough (1982) evaluated the use of night spotlighting by comparing it to a reconstructed population from the well studied George Reserve. He found that males were typically under-represented in spotlight counts and that sighting frequency was lowest during summer months. He cautions that night spotlight counts have several limitations for white-tailed deer research, alluding to concerns with detection probability due to habitat type. While approaches incorporating detection probabilities for transect surveys (Laake et al. 1993) could improve approaches using spotlight counts, roadside counts are biased because researchers cannot randomly place roads (transects) within the study areas.

Roseberry and Woolf (1991) evaluated population reconstruction techniques compared to the CONWR population in southern Illinois and determined that given assumptions regarding lifetime recovery rates for males and females, reconstruction methods provided abundance estimates that coincided with roadside count estimates. Roseberry and Woolf (1991) cautioned that reconstruction could underestimate actual population size. McCullough et al. (1990) applied reconstruction methods to a population of black-tailed deer in California (but see Lubow et al. 1996), while Osborne et al. (1992) applied reconstruction methods to a white-tailed deer population in Georgia with variable success. Williams et al. (2002) stated that use of reconstruction methods to estimate population sizes (and then applying statistical models to this data) should be avoided. Concerns of Williams et al. (2002) with reconstruction methods were; (1)

harvest data is not representative of all mortality factors, and (2) harvest data is biased towards specific age and sex classes (McCullough 1979, Osborne et al. 1992, Williams et al. 2002). Recent maximum likelihood approach to population reconstruction of elk in Idaho (Gove et al. 2002) allows managers to maximize available information taken from harvested individuals combined with estimates of non-hunting mortality, perform model selection procedures, and evaluate critical assumptions regarding reconstruction methods. Approaches such as those shown by Gove et al. (2002) and could provide a valuable management option if applied to white-tailed deer, but could be cost-ineffective if applied at the state level.

Steinhorst and Samuel (1989) and Samuel et al. (1992) developed methods for estimating sighting probabilities for aerial surveys and found little justification for using a perfect visibility model, where detection probability equals 1, and suggested that future surveys should incorporate visibility into population estimation procedures. Trenkel et al. (1997) evaluated methods using aerial line transects for estimating the population size of red deer (*Cervus elaphus*) in Scotland. They found that using aerial line transect methods in conjunction with program DISTANCE (Laake et al. 1993) provided estimates that were agreeable with census methods using simultaneous evaluation by helicopter surveys and ground crews. Aerial transects can provide accurate abundance estimates, however, habitat structure (canopy cover) in the southeastern United States could reduce detection probabilities to levels where aerial transects would not be viable approaches to abundance estimation.

Recent approaches to estimating white-tailed deer population size include the use of distance based sampling methods (Laake et al. 1993), camera surveys (Jacobson et al.

1997), helicopter surveys (Koerth et al. 1997) and combinations of mark-recapture/resight and distance sampling methods (Lopez et al. 2004). Jacobson et al. (1997) evaluated use of camera surveys in Mississippi and found that camera densities of 1 camera per 65 ha gave accurate estimates of population densities. While Jacobson et al. (1997) recaptured 96% and 72% of marked males and females, sex-ratio variation at bait sites could influence density estimates.

Population size is a parameter of interest in population modeling and its importance cannot be overlooked when planning and evaluating white-tailed deer management programs. Although many techniques exist for estimating abundance of wildlife species, few have been applied consistently for estimating white-tailed deer population sizes, and as such few estimates of population size are available in the United States. The limiting factor for application of a majority of these techniques is cost. However, recent advances in density estimation (Laake et al. 1993), and abundance estimation using marked individuals (White 1996) have provided deer managers with new techniques that can provide accurate, unbiased estimates of population size, assuming that underlying model assumptions can be met.

Natural Survival

Knowledge of natural survival rates across age and sex classes for white-tailed deer are essential for understanding population dynamics (DELGuidice et al. 2002). Across the United States a large number of studies have estimated age and sex specific annual and seasonal survival rates for white-tailed deer. DePerno et al. (2000) found that annual survival rates (including harvest) for female white-tailed deer in South Dakota ranged from 0.50-0.62 over their study period, with natural mortality most prevalent

during the spring. Nelson and Mech (1986) found survival rates were approximately two times higher for females than males due to male only harvest and lower wolf (*Canis lupus*) predation on yearling females. Using a model that incorporated seasonal movements, McNay and Voller (1995) estimated annual survival (0.74) for female Columbian black-tailed deer (*Odocoileus hemionus columbianus*). Dusek et al. (1989), Fuller (1990) and Van Deelen et al. (1997) found high survival rates for adult white-tailed deer during the spring/summer (non-hunting) months. Whitlaw et al. (1998) also determined that seasonal survival rates for female white-tailed deer during non-hunting seasons were high (0.84-1.00 in northern New Brunswick; 0.52-1.00 in southern New Brunswick). Seasonal variation in survival rates examined by Nixon et al. (1991) found higher survival across all age classes during non-hunting seasons. These studies contrast with results found by DePerno et al. (2000) whose estimated seasonal survival rates (Fig 2., pp. 1033) were lower during spring than other seasons. Patterson et al. (2002) compared annual survival rates for females (0.804 (SE=0.031)) and males (0.507 (0.076)) in an unprotected location, with annual survival rates in a protected location ((.939 (0.043), 1.0 (0.0) for females and males, respectively). Annual survival rates of females when not exposed to hunting were higher (13%) than those that were still protected but were exposed to hunting (primarily due to illegal harvest). Whereas females were under regulatory protection in Patterson et al. (2002) harvest was still found to be a significant factor on female annual survival rates.

Ditchkoff et al. (2001) found that cause-specific mortality rates for male white-tailed deer differed between age groups (≤ 3.5 years old, ≥ 3.5 years old) with young males (≤ 3.5) more susceptible to human induced mortality while older males (≥ 3.5)

were more susceptible to natural mortality causes. Ditchkoff et al. (2001) concluded that populations with older buck age structure could exclude young males from breeding reducing the likelihood of succumbing to post breeding natural mortality agents. DELGuidice et al. (2002) found that mortality risk was lowest for females between 1.5 and 5.5 years (Fig. 4B, DELGuidice et al. 2002). Estimates from DELGuidice et al. (2002) indicated that harvest accounted for 43% of deer mortalities across the lifetime of study cohorts. Etter et al. (2002) hypothesized that high survival rates (~80%) in urban environments reflected limited hazards in urban areas. Nixon and Mankin (1999) estimated annual survival rates of male white-tailed deer in Illinois and showed declining rates as age class increased (0.56 (0.05) for 2 year olds, 0.50 (0.06) for 3 year olds, and 0.39 (0.09) for 4 year olds).

Several investigators have examined fawn mortality rates and the factors influencing fawn mortality. Taber and Dasmann (1954) found mortality rates for older male fawns was higher in black-tailed deer, and hypothesized that this was possibly due to increasing activity levels and gaining independence from the mothers at early ages. Cook et al. (1971) found that a majority (91%) of fawn mortalities in south Texas occurred in the first few weeks post birth. Cook et al. (1971) estimated fawn loss of 71 and 72% for radio-collared fawns in 1965 and 1966, respectively. Evaluating the effects of predator removal, Beasom (1974) found increased herd productivity (measured in fawn:doe ratio) and hypothesized that intensive predator removal efforts could allow for increased deer densities, given that compensatory sources of mortality were not immediate. Porath (1980) reviewed fawn mortality rates across the U.S. and found that estimated fawn mortality ranged between 8 and 96%. Several authors have elucidated the

impacts of coyote predation as a mortality source for white-tailed deer fawns (Porath 1980, Nelson and Woolf 1987, Lingle 2000). Coyote predation examined in these studies appeared to account for between 22% and 100% of deer fawn mortalities. Predation can also impact the adult segment of the population (Whitlaw 1998). In an experimental reduction of fire ants, Allen et al. (1997) estimated recruitment based on fawn:doe estimates and determined that reductions in fire ants (implying a reduction in predation or injuries) increased fawn recruitment.

A majority of fawn mortalities occur early in life and typically exceeds 50% of the fawns produced annually. Mech and McRoberts (1990) found that fawn survival rates were positively associated with maternal age, which they related to predator defense mechanisms, agreeing with Ozoga and Verme (1986b). Huegel et al. (1985) estimated fawn mortality in Iowa for the first 6-months over a 3 year period at 27.2%. A majority (13.7%) of mortalities documented by Huegel et al. (1985) occurred in the first 30 days postpartum, with no mortalities occurring in the final 30 days. Nixon et al. (1991) estimated fawn (7-12 months) survival rates of 0.88 and 0.95 for males and females, respectively. Estimated mortality from Carroll and Brown (1977) varied based on range conditions (90% mortality during poor range conditions in one site vs. 10% 2 years post during a period of good range condition) but did not differ between sexes. Giuliano et al. (1999) found that survival rates for orphaned fawns were lower than for unorphaned fawns (0.79 versus 1.00), but did not differ by sex, while Etter et al. (1995) found no differences between orphaned and unorphaned female fawns between study sites (0.60 annually; Fig. 2, pp. 443). In a non-hunted population, Long et al. (1998) estimated that

pooled fawn survival to 1 year of age was 0.26 (95% CI = 0.01-0.52) and that survival rates did not differ between sexes.

Density Dependence

Density dependence is defined as a negative relationship between population growth rate and populations size (McCullough 1990). Although density dependence is applied in population models for a wide range of species, detecting and evaluating the effects of density is complicated because little is understood regarding 1) mechanisms that cause density dependence, and 2) relationships between density dependence and population demographic parameters (Bartmann et al. 1992, Lubow 1997, White and Bartmann 1997). Population models that incorporate density dependence imply that the effects of density increase as the population size attains a maximum, defined in terms of ecological carrying capacity (K). Density dependence is an elusive concept, varying both spatially and temporally, and can be difficult to detect in a stochastic environment (McCullough 1990, Bartmann et al. 1992). Several papers and reviews addressed and documented density dependent responses of various demographic parameters of large herbivores (McCullough 1979, Teer 1984, Fowler 1981, Fowler 1987, Bartmann et al. 1992, Getz 1996, Gaillard et al. 2000).

Incorporation of density dependence in population models is often accomplished using logistic models. Logistic models assume that population growth declines quadratically (linearly on a per individual basis) as density of the population increases, although McCullough (1987), Fowler (1981) and White and Bartmann (1997) suggest alternatives to modeling density dependence as a linear relationship. When applying or evaluating density dependence, researchers must determine which demographic factors

are influenced by population size. Eberhardt (1977) outlined a conceptual order for evaluating the influences of density dependence, paying special attention to marine mammals. The order according to Eberhardt (1977) was that first, survival rates of young would decline, followed by shifts in age of first reproduction, declines in adult reproductive rates, and declines in adult survival rates. The rationale for Eberhardt's (1977) hypothesis is that the most direct mechanism behind this order of events is that the limiting factor would be the over-utilization of some resource, mainly food-supply, which has been demonstrated in deer studies (McCullough 1979, Bartmann et al. 1992). Reviews by Fowler (1987) and Gaillard et al. (2000) both agree that initial factors are related to recruitment processes, either in recruitment or postpartum fawn survival, while Bonenfant et al. (2002) showed that pregnancy rates of primiparous females rather than juvenile survival was most sensitive to density. McCullough (1979, 1984) and Teer (1984) both demonstrated density dependence in white-tailed deer recruitment rates, although McCullough's (1979) work was on a fenced population that did not allow emigration while Teer (1984) used index based population estimates, which were subject to considerable bias.

In the most applied experiment to evaluate density dependence, Bartmann et al. (1992) conducted an experimental evaluation of compensatory mortality in mule deer (*Odocoileus hemionus*) found that juvenile survival rates declined as density in experimental pens increased. Bartmann et al. (1992) showed a cause-effect relationship between density and survival rates, however it lacked spatial replication and the population was fenced reducing emigration. Effects of harvest and its resulting impacts on density dependence have been recently evaluated (Solberg et al. 1999), as were

interactions between density and migration (Saether et al. 1999). Several researchers have evaluated effects of climatic variation interacting with density dependence and its resulting influence on population dynamics (Bartmann et al. 1992, Solberg et al. 1999, Mysterud et al. 2000). However, detection of density dependent population responses in deer populations is difficult and as such few research studies have conclusively shown that density dependence (or independence) occurs within deer populations (White and Bartmann 1997). Exact knowledge of density dependent changes in population structure is unknown although evidence exists for reductions in juvenile survival and age of reproduction (Fowler 1987), age specific survival (Forchammer et al. 2001, Festa-Bianchet et al. 2003), sex ratio variation (Kruuk et al. 1999), or compensatory mortality (Bartmann et al. 1992).

Selective Harvest

State agencies use regulatory restrictions on harvest to manipulate white-tailed deer population size, age structure, size structure, and sex ratio (Demarais et al. 2000). Restrictions are set with the intent of manipulating hunter selectivity, thus changing harvest rates of certain age or sex classes to adjust the harvest structure and underlying population structure.

McCullough (1979) discussed how hunter selectivity tended to over-represent harvest of males in intermediate age classes (1.5-4.5 years old), while under-representing harvest of young (<0.5 years) (McCullough 1979, pp. 74). One of the more popular management practices to change hunter selectivity is to restrict harvest of young males using selective harvest criteria (SHC; Carpenter and Gill 1987, Strickland et al. 2001). SHC uses the structure of antler characteristics, typically based on harvested individuals

in the yearling age class. All SHC are based on the underlying assumption that antler characteristics increase to an asymptote, possibly in a curvilinear manner (Scribner and Smith 1990) as individual's age. The phenotypic expression of antler characteristics is influenced by many factors, including age, nutrition, and genetics (Demarais 1999, Demarais et al. 2000).

Phenotype-based restrictions have been evaluated for different species of Order Artiodactyla. Coltman et al. (2003) evaluated trophy hunting for bighorn (*Ovis canadensis*) and found that trophy hunting caused a reduction in traits determining trophy quality (horn length). In a discussion of SHC, Carpenter and Gill (1987) found that while antler restrictions were population management initiatives for several species (mule deer, white-tailed deer, elk). However, Carpenter and Gill (1987) caution that antler restrictions only force harvest pressure to shift by one age class and that the associated costs (population size and age structure) when using antler restrictions were unknown. Carpenter and Gill (1987) state that antler restrictions should be viewed as hypotheses and as such experimental tests should be conducted to determine population responses to different levels of restrictions before implementation. In several studies of regulations on elk, antler restrictions were found not to increase the number of mature bulls (Hernbrode 1987, Vore and DeSimone 1991). Using computer simulations to evaluate genetic differences and harvest potential under SHC for elk, Thenlen (1991) found that antler restrictions (3 point or 5 point) resulted in substantial declines in harvest rates for both total harvest and trophy harvest. Based on his simulation modeling, Thenlen (1991) also concluded that the minimum point plans were all genetically undesirable for production of large antler characteristics. To evaluate the affects of harvest strategy on bull elk

demographics, Bender and Miller (1999) found that a 3-point harvest strategy marginally changed bull mortality and sex ratios, but had little impact on mature bull survivorship. Bender and Miller (1999) note that the regulation only shifted harvest pressure to branch antlered bulls, which agrees in part with conclusions of Carpenter and Gill (1987).

Commonly, deer management practices have focused on encouraging or restricting harvest of individuals whose antler characteristics do not reach a specified level. Harvest of small antlered males has been used to reduce their frequency within the breeding population. Harmel (1983) and Williams and Harmel (1984) concluded that spike antlered males were genetically and nutritionally inferior, and suggest that to improve population antler characteristics males with ≤ 6 points should be selectively removed from the population. Maintaining the selective removal of spike antlered males could impact their future availability in the population (Scribner et al. 1984) while Schultz and Johnson (1992) found that yearling spikes continued to exhibit inferior antler development through the 3.5-year age class.

Habitat conditions have been discussed when describing the incidence of spike (or small antlered) males within a population. Gore (1984) evaluated increased spike harvest and concluded that spike bucks were a symptom of malnutrition due to poor range conditions. Furthermore, Gore (1984) concluded that management practices which selectively harvested spike antlered males would not decrease their frequency unless combined with reduction in population levels. Selective harvest tactics may not be applicable in the face of varying environmental conditions or population densities (Williams and Harmel 1984, Scribner et al. 1984) or across soil quality types (Strickland and Demarais 2000).

The mechanisms and accurate estimates of the allometric relationship between age and antler characteristic remain unknown. Roseberry and Klimstra (1975) found that the greatest increases in antler lengths occurred between 1.5 and 2.5 years of age, with slight increases after 4.5 years of age. However, there was significant variation and overlap in the number of points across and within age classes and Roseberry and Klimstra (1975) stated that over all age classes, number of points was the most variable aspect of antler morphology. DeYoung (1990) evaluated antler characteristics on two Texas ranches and found that male white-tailed deer between 3.5 and 5.5 years old could not be distinguished based on antler characteristics, but could be distinguished from those ≤ 2.5 years old and recommended that if managers would settle for fewer trophy bucks, protection of bucks through 2.5 years old should suffice. Use of antler records from yearling males as criteria for selecting harvest management programs is common, however Lukefahr and Jacobson (1998) determined that heritability for yearling antler characteristics was low, and use of yearling antler characteristics was not supported. Strickland et al. (2001) used simulation modeling to evaluate impacts of SHC on regional antler characteristics in Mississippi white-tailed deer and determined that SHC could protect young males but the efficiency of SHC varied regionally. Although Strickland et al. (2001) suggested that there were numerous factors that could impact antler characteristics; none were evaluated in the simulation modeling approach.

Experimental tests of management programs using SHC have not been conducted in the United States. Thus, we have limited knowledge of the relationship between antler characteristics, age, nutrition, and genetics. While management emphasis in the southeastern United States has recently focused on increasing male population age

structure using SHC, little progress has been made as previous evaluations have shown that these criteria do not increase population age structure, instead only shift harvest pressure up one age class (Carpenter and Gill 1987). Therefore, management emphasis in the southeastern United States should be placed on evaluating buck age structure and nutritional limitations before implementation of selective harvest practices (Demarais 1999).

MODELING APPROACH

When structuring any modeling exercise to address population dynamics, an initial decision must be made concerning the proposed model's purpose (McCallum 2000). Holling (1966) suggested that models examining population dynamics exist on a continuum. At one extreme are empirical models, which are used to make predictions regarding states of nature, while at the other extreme are abstract models that attempt to provide general insights (Holling 1966, May 1974, Nisbet and Gurney 1982, McCallum 2000). Predictive (empirical) models are applied frequently in ecological studies, as they attempt to forecast ecological states (McCallum 2000, Burnham and Anderson 2002). Quantitative forecasts from predictive models are used to provide wildlife managers with realizations of ecological processes.

Lancia et al. (2000) hypothesized four necessary methodological assumptions for estimating population parameters of large mammals. They state that selected methods for population parameter estimation should: "(1) have assumptions that can be met, (2) provide precise estimates, (3) provide adequate information to make informed decisions, and (4) be cost effective (Lancia et al. 2000, pg. 81)."

Use of predictive models requires estimation of a larger number of parameters than necessary for abstract models (McCallum 2000, Burnham and Anderson 2002, Williams et al. 2002). Creation of population dynamics models that accurately describe or predict an ecological system's state necessitates estimation of parameters that describe those system states. Nichols et al. (1992) and White (2000) suggested that when modeling a population or applying a model to a population, model parameters should be estimated from field data on that population. While use of parameter estimates from rigorous, statistically defensible studies for populations of interest are preferred (McCallum 2000, Williams et al. 2002) it is impractical to address all plausible mechanisms influencing the population or ecological system of interest across the short time frame of most ecological studies. Therefore, researchers incorporate relevant information regarding parameter estimates and associated variance estimates from other studies to parameterize predictive models when data is lacking.

Accounting for parameter uncertainty

Effective population management requires that managers incorporate information on underlying population processes in conjunction with management policies when constructing management programs. One often cited population model is the simple exponential model (Gotelli 1995, Williams et al. 2002):

$$N_{(t+1)} = N_{(t)} + rN_{(t)} \quad (1)$$

where $N_{(t)}$ is abundance at time t and r is per capita recruitment rate. In this simple population model, with assumptions regarding the initial values of $N_{(t)}$ and r , the population size at time $(t+1)$ is deterministic because neither parameter exhibits randomness and the only information needed to predict population size at $(t+1)$ is the

population at time (t) . However, wildlife population dynamics are influenced by many sources of uncertainty (Trenkel et al. 2000), and models with such simplistic structure do not exhibit generality (Dunham and Beaupre 1998) and therefore have limited usefulness.

To be realistic, population models must include simultaneous interactions between deterministic and stochastic components (Lande et al. 2003) as both influence population dynamics differently. Although stochastic population modeling is a powerful tool for evaluating wildlife population dynamics (Lande et al. 2003, Phillips and White 2003), it is infrequently applied in wildlife sciences to assist in planning and evaluating management options. Stochastic population modeling provides researchers with a method for investigating temporal changes in wildlife populations (Engen et al. 1998, Lande et al. 2003). Stochastic variation in population models is accounted for by incorporation of demographic and environmental variability, either separately or as jointly interacting components of the population processes. Demographic stochasticity, as defined by Engen et al. (1998), is the variation between individuals, and refers to the independence of mortality or recruitment events between individuals in a population. Environmental stochasticity, also as defined by Engen et al. (1998), is characterized as the variation in demographic parameters based on characterization of the environment, and refers to changes over time in the rates of survival and recruitment across individuals in the population. Small populations are most impacted by the effects of demographic stochasticity (variation in birth and death rates), while larger populations are most impacted by environmental variation (Lande et al. 2003). Impacts of demographic stochasticity are reduced as population size increases (Engen et al. 2003). However, Engen et al. (2003) found that for small populations with polygamous mating systems,

fluctuations in sex ratio may lead to larger demographic variation, and that a bias in sex ratio could endure over time, complicating population processes and reducing certainty in modeling. Because populations fluctuate due to biotic and abiotic processes, incorporation of stochasticity into the modeling process is needed by managers when modeling population dynamics.

Because the fundamental unit in ecology is the individual organism, individual variability is also an important component of most ecological systems (Dunham and Beaupre 1998, Pfister and Stevens 2003). Individual variability in ungulates influences reproductive success (Clutton-Brock et al. 1982), neonatal mortality (Verme 1962, 1965), fawn survival (Bartmann et al. 1992), sex ratio (Verme 1983), and breeding synchrony (Verme 1965). Variability among individuals should play an important part in modeling population dynamics, especially for populations under a selective harvest regime (Ratner and Lande 2001, Strickland et al. 2001). As many current management practices for white-tailed deer are based on phenotypic characteristics, individual variation in these characteristics can have extensive ramifications, especially when selective pressure (e.g. harvest) depends upon whether an individual is protected or exploited.

Introduction to the problem and approach

Historical frameworks used by white-tailed deer managers to evaluate harvest management strategies and population goals are simplified approaches to a complex system. A modeling approach is needed that allows for the combination of empirical and abstract population models for making quantitative assessments regarding white-tailed deer population responses to management actions. Limited demographic information across the range of white-tailed deer necessitates an approach that allows managers to

incorporate what is known about white-tailed deer population dynamics with the effects of regulatory restrictions to assist in evaluating population response to management programs.

To evaluate the effects of regulatory programs on the age and sex structure of white-tailed deer populations in Arkansas, I recast a stochastic age- and sex-structured white-tailed deer population model into a probabilistic framework. Probabilistic networks, also known as Bayesian Belief Networks (BBNs), probabilistic causal networks, or belief networks (Pearl 1988, Charniak 1991, Haas 1991, Marcot et al. 2001, Peterson and Evans 2003) are a special class of graphical models that allow modelers to probabilistically represent causal relationships between biological parameters. While probabilistic models are common in the artificial intelligence community, there have been few applications of probabilistic models to wildlife sciences. Lee and Reiman (1997) developed a Bayesian viability assessment procedure (BayVAM) to evaluate land use risks to salmonids in the Pacific Northwest, which was also applied by Shepard et al. (1997) to evaluate extinction risk (persistence probability) of westslope cutthroat trout (*Oncorhynchus clarki lewisi*) in Montana. Marcot et al. (2001) reviewed techniques for applying Bayesian Belief Networks (BBNs), and developed a BBN to evaluate viability for a Townsend's big-eared bat (*Corynorhinus townsendii*) based on environmental correlates at 3 geographical levels. BBNs have been used to model habitat capability for 3 species of ungulates (white-tailed deer (*Odocoileus virginianus*), elk (*Cervus elaphus*), and mule deer (*Odocoileus hemionus*)) across the interior Columbia River basin (Lehmkuhl et al. 2001). Also in the interior Columbia River Basin, Raphael et al. (2001) evaluated effects of different land management alternatives on terrestrial

vertebrates of concern. Raphael et al. (2001) projected population outcomes (defined as environmental outcome and population outcome) for 28 species of concern across two time frames (historical and current) and three management alternatives. Hass (1992) used Bayesian network models to assist in making forest management decisions; while Haas (1991) and Haas et al. (1994) created and applied BBN models to evaluate aspen stand growth after a “stand regeneration event (SRE), such as a clearcut (Haas et al. 1994, pg. 16).” Using a decision network incorporating human dimensions information along with underlying population processes, Peterson and Evans (2003) developed a BBN to assist fisheries managers in Georgia in evaluating effects of different length limit decisions on large mouth bass (*Micropterus salmoides*) angler satisfaction. Steventon et al. (2003) used BBNs to evaluate long-term risk assessment of Marbled Murrelets (*Brachyramphus marmoratus*) in coastal British Columbia. Incorporating a habitat linked population viability analysis into a BBN, Steventon et al. (2003) found that habitat supply and quality (which Steventon et al. (2003) defined as “nesting density”), when combined with survival and reproductive rates (defined as affected by future as-sea conditions), were the most important predictors of projected population outcomes.

Because there is a limited number of studies that have used this approach, variation between study species and modeling constructs are limited. Several general examples have focused on large-scale land management practices by incorporating GIS proxy variables into the modeling scenarios (Marcot et al. 2001, Raphael et al. 2001, Lehmkuhl et al. 2001). Several applications of BBNs incorporate biological processes using stochastic population simulation models, such as described by Lee and Hyman (1992), to parameterize the probabilistic networks (Lee and Rieman 1997 (BayVAM),

Shepard et al. 1997 (BayVAM), Steventon et al. 2003, Peterson and Evans (2003)).

However, a majority of these approaches only simulate the female segment of the population, while not accounting for effects of the male segment on biological processes. This approach is done to simplify the modeling procedure, by reducing the need to track age- and sex-specific parameters over model runs. For wildlife populations, especially those managed using age- and sex-specific harvests, it becomes necessary to track and evaluate parameters for both sexes within the modeling framework, thereby increasing model complexity.

By recasting the white-tailed deer population model as a BBN, managers will be able to evaluate the influence of population demography, regulatory restrictions, and spatial scale on the age and sex structure of white-tailed deer populations in Arkansas. The BBN framework allows managers to model linkages between biological and regulatory factors, incorporate and evaluate uncertainty in parameter estimates, and provides a potential framework for adaptive management programs.

Using the techniques and information discussed above, my dissertation will specifically address the effects of a selective male harvest strategy on white-tailed deer population age structure and sex ratios at multiple spatial scales in Arkansas under parameter uncertainty. In Chapter I provide a review of current knowledge of white-tailed deer population processes and modeling approaches. Chapter II evaluates the combined influence of localized white-tailed deer management and regulatory actions on the age and sex structure across multiple scales. Chapter III addresses several Arkansas Game and Fish Commission research hypotheses of interest using the probabilistic

model. Chapter IV evaluates the completed research project, evaluates the modeling approaches, and discusses future research avenues.

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CHAPTER II. MODELING OF WHITE-TAILED DEER POPULATIONS IN ARKANSAS: EVALUATING POPULATION DYNAMICS AND REGULATORY STRUCTURE IN A GRAPHICAL FRAMEWORK AT MULTIPLE SCALES

ABSTRACT

White-tailed deer (*Odocoileus virginianus*) management is a difficult challenge for wildlife managers, as they are required to plan and evaluate management actions under considerable levels of uncertainty concerning population parameters. Variation in population processes over multiple spatial scales has limited the ability of managers to spatially extend relevant data for management planning. To assist managers in Arkansas with decision processes, I developed a spatially explicit stochastic population simulation model to evaluate impacts of variation in population dynamics and 2 periods of regulatory restriction on white-tailed deer population age structure and sex ratio at multiple scales in Arkansas. I then recast the stochastic population models in a graphical framework using a Bayesian Belief Network (BBN) to examine predictive ability given parameter uncertainty and stochastic variation in population dynamics. Residual (post-harvest) population sex ratio was most sensitive to pre-harvest sex ratio and initial sex ratio at the local scale (77% and 58% reduction in uncertainty, respectively) and to pre-harvest sex ratio (15% reduction in uncertainty) at higher scales. Harvest sex ratio had limited influence on predicting residual population sex ratio ($\leq 10\%$ at all scales). At the local scale, under historical regulations the residual population structure for both sub-adult and adult males exceeded 5% of total population size in $\leq 9\%$ and $\leq 17\%$ of simulated responses (cumulative probabilities of 0.91 and 0.73, respectively) and

exceeded 10% of total population size in $\leq 4\%$ of simulated responses. Under current regulations, residual population structure exceeded 5% of the total population size in $\leq 10\%$ and $\leq 32\%$ and exceeded 10% of the total population in $\leq 5\%$ of simulated responses. At the county level and above, under historical regulations, yearling males exceeded 10% of total population size in $\leq 1\%$ of predictions, but under current regulations, yearlings exceeded 10% of total population size in 30% of responses (Fig 7). Model predictions at the county level indicated that residual sub-adults exceeded 10% of the total population size in $\leq 1\%$ under historical regulations, and never under current regulations. My results indicated that benefits of protecting yearlings using antler restrictions were lost after age class transition, and that the restriction shifted population age structure to levels below those exhibited during periods of less regulation. I recommend that long-term experimental studies evaluating mechanistic relationships between population parameters at multiple scales under different harvest management regimes be implemented. These parameters could be estimated in conjunction with short-term research evaluating other white-tailed deer population processes preferably through application of mark-recapture, mark-resight techniques for vital rate estimation, as well as transect based distance sampling approaches for density and abundance estimation. I suggest that probabilistic graphical models provide an alternative to current approaches for white-tailed deer management planning and evaluation, allowing managers to combine available biological information with expert opinions in a quantitative framework that explicitly represents where knowledge is lacking.

Optimal management of biological systems is a difficult task for wildlife managers. Recently, increased attention has been paid by ecologists to determine how emergent properties can differ between populations across spatial and temporal scales (Wiens 1989, Levin 1992, Hanski and Simberloff 1997, Ray and Hastings 1996, Donalson and Nisbet 1999, Royle and Dubovsky 2001). As no ecological system has a single characteristic scale at which all processes operate (Carpenter 1996, Coulson et al. 1999), managers must evaluate population dynamics at multiple scales to adequately plan management actions. Management for white-tailed deer (*Odocoileus virginianus*) is intended to manipulate population characteristics such as abundance, age structure, and sex ratio (Demarais et al. 2000). The importance of spatial scale when modeling ungulate population dynamics (Healy et al. 1997, Coulson et al. 1999, Mysterud et al. 2000), and scale dependent evaluations of harvest (McCullough 1996) has highlighted scale as an important factor for planning and evaluating white-tailed deer population dynamics.

Categorizing population patterns is innately related to spatial scale. Modeling approaches over large scales exhibit high levels of aggregation, and are more robust to error propagation than models at the individual level (Pascual and Levin 1999), but scale dependent variation can obscure population processes (Ray and Hastings 1996). As wildlife management requires spatially extending observations beyond study locations (McKenny et al. 1998), scaling issue should be incorporated into white-tailed deer management planning and evaluation procedures. Techniques for spatially extending white-tailed deer biological information to assist with constructing and evaluating harvest management programs are unavailable. Studies on population parameter relationships have been conducted at small scales (McCullough 1979, Bartmann et al. 1992).

Evaluations of harvest management practices are also primarily conducted at small scales (Jacobson 1992, Ditchkoff et al. 1998, 2001, Jenks et al. 2002), or are scale invariant (Hansen 1998, Xie et al. 1999, Strickland et al. 2001). However, few research studies have attempted landscape scale experiments, and as such the uncertainty due to lack of information at multiple spatial scales has reduced the ability of managers to plan and evaluate management decisions (McShea et al. 1997).

Currently, few model driven methods for monitoring and evaluating white-tailed deer management programs are in place across the United States. Limited demographic information and uncertainty in parameter estimates (Trenkel et al. 2000) has required most management planning to use information collected from harvested deer (Roseberry and Woolf 1991, Carpenter 1996), which can be a biased representation of the true population (Ditchkoff et al. 2000). Management planning using data from harvested individuals does not account for variable population processes and have had limited success (Roseberry and Woolf 1991, Lubow et al. 1996).

Use of data from harvested individuals for planning and evaluation of management strategies for white-tailed deer has become more confounded recently given the proliferation of various selective harvest criteria (SHC; Carpenter and Gill 1987, Strickland et al. 2001). In Arkansas, the SHC used is a minimum point restriction, requiring hunters to restrict harvest to those male individuals that whose antler characteristics exceed the minimum standard of 3-points on 1 main beam. The intent of Arkansas's SHC was to shift harvest pressure from young to older age classes, which was expected to increase population age structure to levels more representative of natural populations (Ditchkoff et al. 2001). Limited evaluations of SHC have shown that SHC

can change the harvest age structure (Carpenter and Gill 1987, Jacobson 1992); however no studies have shown that SHC directional shifts in underlying population age structure.

Population models are commonly used to construct and evaluate harvest regulations for game species across the United States (White et al. 2001, White and Lubow 2002). Population parameter estimates are limited across the white-tailed deer's range, and those available could exaggerate certainty (Lee 2002). Although parameter estimates from rigorous experimental studies for populations of interest are preferred (Nichols et al. 1992, McCallum 2000, White 2000, Williams et al. 2002), it is impractical to address of interacting ecological mechanisms across the short time frame of most ecological studies. Thus, researchers frequently incorporate relevant information regarding parameter and associated variance estimates from other studies to parameterize predictive models (Jorgensen 1993). While often overlooked as a management option (Phillips and White 2003), stochastic population modeling (SPM) provides managers with an alternative to current approaches to white-tailed deer management. SPM allows managers to evaluate simultaneous interactions between deterministic and stochastic model components (Lande et al. 2003), temporal changes in population size and structure (Engen et al. 1998, Lande et al. 2003), and approach management planning using what-if scenarios (Walters and Gross 1972).

I developed a stochastic age- and sex-structured population model to evaluate the impact of SHC on Arkansas white-tailed deer population age structure and sex ratio while accounting for various levels of parameter uncertainty. My modeling approach incorporated available biological information on white-tailed deer population dynamics collected in Arkansas, parameter estimates taken from other white-tailed deer research

studies, and expert opinions from Arkansas Game and Fish Commission (AGFC) personnel. My approach was designed to (1) simulate white-tailed deer population dynamics at multiple spatial scales in order to evaluate white-tailed deer population responses to management restrictions under parameter uncertainty, (2) to demonstrate an application of stochastic population modeling incorporating demographic and environmental variation and the resulting impacts on white-tailed deer population dynamics, (3) evaluate at which scale white-tailed deer managers in Arkansas can adequately plan and evaluate management strategies, and (4) to provide relevant output to be used in a graphical modeling approach allowing the AGFC to adequately plan future management strategies under various levels of parameter uncertainty.

POPULATION MODEL

Model Structure

The underlying model was developed as a stochastic age- and sex-structured population simulation model written in program R (R Core Development Team 2004). The population model was represented mathematically in several sections that simulated a 1-year time step. The model tracks both sexes and 5 mutually exclusive age classes: (juveniles (birth to recruitment), fawns (6 months old), yearlings (1.5 years old), sub-adults (2.5 years old) and adults (≥ 3.5 years old)). Newborn fawns were modeled independently of other age classes from birth until recruitment into the fall (fawn) population because considerable variation exists in juvenile survival rates and sex ratios (Carroll and Brown 1977, Verme 1983). The 4 non-juvenile age classes were selected as (1) female fecundity varies across age classes, (2) limited numbers of males reach age classes ≥ 3.5 years old in heavily hunted populations (Ditchkoff et al. 2001), and (3) the

SHC used by Arkansas focused on shifting pressure from the 1.5 year old male age class to the 2.5 year male age class.

After the initial population was defined, seasonal survival rates were applied for each age-sex combination. Surviving females contributed to recruitment where juveniles were produced (based on age specific recruitment rates) and recruited (based on fawn survival rates) into the fawn population while the surviving population transitions 1 age class. Annual harvest (legal and ancillary) was separated by age and sex and was applied after age class transition. The residual population (post-harvest population by age and sex) becomes the initial population structure for the following time step.

Mathematically, the model represents the change in the population through time of both sexes for 5 mutually exclusive age classes; juveniles, fawns, yearlings, sub-adults, and adults where juvenile gender was not specified until transition into the fawn population. I structured the initial population into 4 age classes (fawns (F), yearlings (Y), sub-adults (S), and adults (A)), and seasonal survival rates were applied to both sexes (males (B), females (D)) across all age classes using the following expressions (following Phillips and White (2003)) (Fig. 1.):

$$N_{YB}(t_{PRE}) = \text{binom}(N_{FB}(t), \hat{S}_F(t)),$$

$$N_{SB}(t_{PRE}) = \text{binom}(N_{YB}(t), \hat{S}_Y(t)),$$

$$N_{AB}(t_{PRE}) = \text{binom}(N_{AB}(t), \hat{S}_A(t)) + \text{binom}(N_{SB}(t), \hat{S}_S(t)),$$

$$N_{YD}(t_{PRE}) = \text{binom}(N_{FD}(t), \hat{S}_F(t)),$$

$$N_{SD}(t_{PRE}) = \text{binom}(N_{YD}(t), \hat{S}_Y(t)),$$

and

$$N_{AD}(t_{PRE}) = \text{binom}(N_{AD}(t), \hat{S}_A(t)) + \text{binom}(N_{SD}(t), \hat{S}_S(t)),$$

where (t_{PRE}) represents population structure at an intermediate time prior to harvest, and $\hat{S}_F, \hat{S}_Y, \hat{S}_S, \hat{S}_A$, are seasonal survival rates for fawns, yearlings, sub-adults, and adults, respectively. After application of seasonal survival rates, those surviving females contribute to recruitment processes based on the following equations:

$$N_J(t_{PRE}) = \sum_1^{N_D^A(t_{PRE})} \text{pois}(\hat{R}_D^A(t), \hat{S}_J(t)),$$

where $N_J(t_{PRE})$ is the number of newly produced offspring, N_D^A represents the number of surviving females in the A^{th} age class in time t , $\hat{R}_D^A(t)$ is the mean annual recruitment rate of females in the A^{th} age class (assuming female fecundity was based on previous season age class), and $\hat{S}_J(t)$ is the juvenile (postpartum) survival rate until recruitment into the fawn age class. Surviving juveniles were separated by sex into fawn age class dependent on fawn sex ratio (fsr):

$$N_{FB}(t_{PRE}) = \text{binom}(N_J(t_{PRE}), (fsr)),$$

$$N_{FD}(t_{PRE}) = \text{binom}(N_J(t_{PRE}), (fsr)),$$

where $N_{FB}(t_{PRE})$ and $N_{FD}(t_{PRE})$ is the number of males and females recruited, respectively, from the juvenile to fawn age class prior to harvest. The equations I used to express harvest were:

$$\hat{H}_{Age}^{Sex}(t) = (H_{Age}^{Sex}(t) * \tau_{Age}^{Sex}(t)),$$

$$N_{Age}^{Sex}(t+1) = \text{binom}(N_{Age}^{Sex}(t_{PRE}), \hat{H}_{Age}^{Sex}(t)),$$

where $\hat{H}_{\text{Age}}^{\text{Sex}}(t)$ is the estimated harvest rate of white-tailed deer, $H_{\text{Age}}^{\text{Sex}}(t)$ represents estimated harvest (% by age within sex class based on biological data collected by AGFC) of white-tailed deer by age and sex class during t , and $\tau_{\text{Age}}^{\text{Sex}}(t)$ is a scale multiplier applied to estimated harvest which allows the harvest rate to range from 25% to 200% of the proportion harvested in each male age class. The residual (post-harvest) population ($N_{\text{Age}}^{\text{Sex}}(t+1)$) then becomes the initial population size estimates for each age- and sex-combination for the next time step.

Initial Parameter Estimates and Assumptions

Available information regarding population size and age structure, age- and sex-specific survival rates, age- and sex-specific recruitment rates, and harvest information were used to model deer population dynamics in Arkansas (Tables 1 and 2). I modeled deer populations at the local scale using biological information from hunting camps registered in the Arkansas Deer Camp Program (DCP) as well as at the county scale as these were the 2 scale levels at which most biological information was classified. Evaluations at higher spatial resolutions can be accomplished using these modeled populations in a probabilistic framework.

In an optimal modeling situation, age- and sex specific abundance estimates would be available. However, across the deer's range this information is unavailable (McShea et al. 1997). Thus, I developed initial population structure estimates using combinations of initial densities, population age structure, and population sex ratio based on expert opinion provide by AGFC staff. At the local scale, abundance was modeled as the product of a uniform random variable (expressed as deer/ha) and estimates of hunting camp size bounded at the minimum and maximum camp size in Arkansas (unpublished

data). Arkansas has 4 distinct physio-geographic regions, each exhibiting sections of spatially homogeneous and heterogeneous habitats. To account for abundance variation due to habitat structure, I first constructed county level (km^2) habitat suitability index by classifying 1999 landscape images (GeoStor, Center for Advanced Spatial Technologies, University of Arkansas) into 4 classes (Urban-Water, Oak-Hickory Forest, Pine-Forest, and Agricultural-Herbaceous). Expert opinion provided by AGFC staff specified a deer capacity index (0, 1.0, 0.85, and 0.4, respectively) for each class. The product of the deer capacity index and percent habitat class in each count provided a habitat based deer capacity estimate. I then defined a maximum deer per county estimate as the product of a Poisson random variate (evaluated in deer/ km^2) and county size (km^2). The product of the deer capacity estimate and the maximum deer/county provided an estimate of initial population abundance.

In wildlife studies, information population age structure is limited (Trenkel et al. 2000). Initial estimates for female population age structure were constructed using age structure information from females harvested in spring 2001-2004 during a recruitment study (AGFC unpublished data). Age structure for the male population was based on expert opinion provided by AGFC staff (unpublished data). I used a random draw from a Dirichlet (Schervish 1995) to incorporate variation in initial age structure estimates. Initial population sex ratio was drawn from a uniform distribution based on information collected during annual spotlight counts conducted by AGFC staff (unpublished data).

Survival and Recruitment

Annual estimates of survival rates were not available for white-tailed deer across Arkansas. Thus, seasonal survival rates were modeled using estimated ranges of survival

rates for white-tailed deer. Age specific survival rates (S_0) were drawn from a uniform distribution and modeled as a density dependent process. Survival rates were equal for fawn-yearling and sub-adult-adult, differed between classes, and were applied before recruitment so only surviving females could contribute to recruitment processes.

Currently few estimates of density dependence in survival rates are available for deer in the United States. Thus, I adopted model forms and estimates from Bartmann et al. (1992) and Lubow et al. (1996). At the local scale, density-dependent in non-juvenile survival rates was modeled using the equation:

$$\hat{S}_{Age}(t) = \frac{1}{1 + e^{-(\alpha - 0.0691D(t))}}$$

where the model parameter $\alpha = \ln\left(\frac{S_0}{1 - S_0}\right)$ defines the intercept at $D(t) = 0$ (Lubow et al. 1996) and 0.0691 is a slope estimate adjusted for difference in spatial area. At the county scale, the model form was the same, except the slope estimate was changed to 0.00691 to account for spatial area.

Juvenile recruitment into the fawn class was modeled using a combination of surviving females, female recruitment rates, and juvenile survival rates. I used AGFC fetus count data (AGFC unpublished) to estimate juvenile recruitment (fawns per female) for female age classes. To stay consistent with the stochastic, discrete characteristics of the model, juvenile recruitment was modeled as a Poisson random variate with parameter $\lambda_A =$ average number of fetuses/female of the A^{th} age class. Juvenile survival rates (S_J) were drawn from a normal distribution ($\bar{x}=0.5$, $(SE=0.1)$) and modeled as a density dependent process. Transitions from juveniles to the fawn age class for both scales were modeled using a density-dependent process:

$$\hat{S}_j = \frac{1}{1 + e^{-(\alpha - 1.95D(t))}},$$

where the model parameter $\alpha = \ln\left(\frac{S_j}{1 - S_j}\right)$ defines the intercept at $D(t) = 0$ (Lubow et al. 1996) and 1.95 is a slope estimate adjusted for difference in spatial area. At the county scale, the model form was the same, except the slope estimate was changed to 0.0195 to account for spatial area. While estimates from Bartmann et al. (1992) and Lubow et al. (1996) were constructed from data on mule deer (*Odocoileus hemionus*), they are currently the best available estimates for density dependent mortality in United States ungulates and as such I chose to use these functional forms rather than an untested form (see Xie et al. 1999, Peterson et al. 2003).

Environmental Influences

I modeled the effects of environmental variation in 2 separate ways. Based on suggestions from AGFC staff, occurrences of environmental variation were based on a 10% deviation in annual spring/summer precipitation. A random draw from a Bernoulli distribution based on the occurrence of 2 consecutive periods of deviation in precipitation over the past 20 years was used to define environmental influences. Environmental effects were modeled to influence both fawn survival rates during the current time step (Carroll and Brown 1977), and fetal sex ratio in the following time step. In the presence of environmental effects, the estimates for juvenile survival (S_j) were adjusted downward as the product of juvenile survival and a random draw from a Uniform distribution bounded at (0.25 and 0.75). If breeding females are nutritionally stressed due to reduced forage availability, typically due to environmental conditions (Carroll and Brown 1977, Teer 1984, Ginnett and Young 2000), fetal sex ratios will tend to skew more towards

males (Verme 1965, 1967, 1983, 1985). Thus, events occurring during the current year would influence fetal sex ratio in the following year based on my expectation that nutritional deficiencies would lag 1 year (McCullough 1979).

Sex Ratio

Within the model structure, sex ratio variation (expressed as %male) was incorporated in 2 ways. Initial population sex ratio (sex ratio at model initiation) was drawn from a uniform distribution based on information collected during annual spotlight counts conducted by AGFC staff (unpublished data). Because there is evidence of considerable variation in fetal sex ratio (Verme 1965, 1967, 1969, 1983), fetal sex ratio variation was incorporated into the recruitment process. In situations where during the preceding model year an environmental event occurred, surviving juveniles were recruited into the fawn population at levels that were skewed towards male offspring. In those cases where the prior model year did not include an environmental event, surviving juveniles were recruited at levels skewed towards females. For this segment of the model, I assumed that mortality rates did not differ between sexes (Carroll and Brown 1977, Etter et al. 1995, Giuliano et al. 1999). I used the commonly assumed optimal sex ratio of 1 male per 2 females (Demarais et al. 2000) for evaluation of population sex ratio response to regulations.

Incorporating Harvest

Harvest (legal and ancillary (non-legal)) was modeled as a density independent process and was assumed to be additive to natural mortality (Dusek et al. 1992). Estimates for legal harvest at the local scale were based on biological information collected from harvested individuals on hunting camps registered in the Arkansas DCP,

whereas estimates for the county scale were based on biological information collected at the county level by AGFC monitored check stations. Because regulatory structure, localized management practices, and property ownership class could influence harvest (unpublished data), at the local scale available biological data was classified into 12 combinations (Scenarios) based on these categories. For county level analysis, biological data was classified by regulatory structure. Regulatory structure was defined as 2 periods: (1) In Effect, or periods of harvest data collection where the antler restriction was in effect, and (2) Not In Effect, or periods of harvest data collection where the antler restriction was not in effect. At the local scale, localized management was classified in 2 categories based on whether hunting camps were conducting harvest management in excess of state regulations, or were not conducting harvest management in excess of state regulations (unpublished data). Harvest data were also classified based on property ownership class: (1) property privately owned by camp members, (2) property leased by camp members, or (3) timber industry property leased by camp members (unpublished data). Harvested deer were aged by AGFC staff or trained hunting camps members based on tooth wear and replacement (Severinghaus 1949). There is considerable variation associated with this technique as deer age, across habitat condition, and due to measurement error (Gee et al. 2002). Thus, I classified white-tailed deer into 4 age categories for each sex in order to reduce this variability. At the local scale, harvest was estimated for age-sex combinations specific to one of the 12 scenarios in the model. In several cases, biological data for females were not available at the county level for both periods of regulatory restriction. In those situations, age structure values were based on information collected at the regional level was used, assuming that age structure of

female harvest was equal between periods of regulation. To check this assumption, a complete subset of data collected from hunting camps on Anderson-Tully Inc. (M. Staten, Anderson-Tully, Inc., personal communication) properties was analyzed using a generalized linear model with a Poisson distribution (GENMOD, SAS 2000). I tested if female harvest by age was consistent between the 2 periods of regulatory restriction.

I incorporated variation in the harvest estimates by randomly drawing from a Dirichlet distribution [$\text{Dir}(\alpha_1 + x_1, \dots, \alpha_k + x_k)$] having posterior distribution:

$$\alpha \prod_{i=1}^4 \rho_i^{x_i + \alpha_i - 1},$$

with parameters; α = prior probability (modeled as a uniform prior = 1), ρ_i = harvest probability for the i^{th} age class, and x_i = observed frequency of harvest for the i^{th} age class.

Although harvest data provide valuable information on the harvest population, they are inherently skewed towards certain age-sex combinations (McCullough 1979, Carpenter 2000) and provide questionable information on underlying population structure. The assumption of proportional harvest is not practical for selectively harvested species. To account for differences between estimates collected from harvest deer and the rate of harvest by age and sex, I applied a multiplicative relationship into each simulation scenario where estimates for the rate scale were constructed based on AGFC staff expert opinion. I modeled ancillary loss to occur after harvest and considered ancillary loss additive to both natural and harvest mortality. Because limited information exists to quantify the level and selectivity of ancillary loss (Ditchkoff et al. 1998), estimates for ancillary loss used in the model were based on expert opinion

provided by AGFC staff. Estimates of ancillary loss were equal for fawn-yearling and sub-adult-adult classes, differed between classes, and were applied after harvest.

Model Stochasticity

I incorporated demographic stochasticity into the modeling procedure using discrete processes based on Binomial (binom) or Poisson (pois) random variates. I modeled survival rates, harvest rates (both legal and ancillary), and fawn sex ratios as Binomial random variates where each individual in the population either survived (p) or died ($1-p$) (or was male/female) based on the estimated parameter over the 20-year model run (Phillips and White 2003). I modeled birth rates using a Poisson distribution with mean (λ_A) equal to the average number of fetuses produced by females in the A^{th} age class. Across model runs, average number of fetuses was constant, but birth rates were variable dependent on random draws from a Poisson distribution. Thus, the number of individuals born, surviving, or harvested exhibited variability within each model run based on my inclusion of demographic variation.

PROBABILISTIC MODEL

Use of population models has become common when planning wildlife management practices (White and Lubow 2002). Across the range of white-tailed deer, sufficient data are lacking to evaluate model structure and test assumptions regarding underlying relationships between population parameters. The uncertainty associated with model form, as well as uncertainty associated with variation in population vital rates limits the ability of managers to predict future system states (Lee and Rieman 1997, Marcot et al. 2001, Lee 2002). Managers need the ability to accurately represent uncertainty in parameter estimates and how this uncertainty influences predictive ability

(Borsuk et al. 2004). Thus, I developed a probabilistic graphical model in NETICA (Norsys. Software Corp.) that provides deer managers in Arkansas with a new method for planning and evaluation of white-tailed deer management practices. Probabilistic graphical models, also known as Bayesian Belief Networks (BBNs) (Pearl 1988, Marcot et al. 2001) are a class of graphical models that allow managers to probabilistically represent causal relationships between biological parameters.

The general design of a BBN begins with a graphical structure that represents system variables using boxes (nodes) and arrows (links) (Steventon et al. 2003, Borsuk et al. 2004). Each node represents a biological or regulatory variable while the arrows represent the conditional probabilistic relationship between these factors (Lee and Rieman 1997, Peterson and Evans 2003). Input nodes, or those nodes which have no predecessors (Charniak 1991), specify marginal (unconditional) probabilities, or the likelihood that the input parameter is in a specific state. Non-root node values are described by conditional probability tables (CPT) (Marcot et al. 2001) which represents the likelihood that the parameter is in a specific state, conditional on the state of the input nodes affecting it (Marcot et al. 2001, Lee 2002). Commonly depicted a probability histograms, resulting estimates represent the “degree of belief” or probability expressed as a percentage for response value given the value of the input nodes (Lee and Rieman 1997, Marcot et al. 2001, Lee 2002). When node values are concentrated within a small range of values, it represents a higher belief in the probability of response falling within a smaller range (Lee and Rieman 1997).

When information is incorporated into the model structure, estimated posterior probabilities represent the likelihood that a parameter is in a specific state, given the input

parameters, conditional relationships, and probabilistic rules based on Bayes (1763; Price¹) theorem:

$$P(\theta | X) \propto P(\theta)P(X | \theta),$$

where the posterior probability of a random variable having value θ given the occurrence of X (data) is proportional to the probability of the random variable θ times the likelihood of X occurring conditional on the value of θ (Lee 1997).

Conditional Probability Estimation

Quantification of conditional probabilities for node relationships can be accomplished in several different ways, including, (1) direct entry of estimates into the CPT, (2) through mathematical expressions of biological relationships (converted to CPT by NETICA) (Borsuk et al. 2004), or (3) being read into the BBN as a case file (Lee and Rieman 1997, Peterson and Evans 2003, Steventon et al. 2003). In order to estimate conditional probabilities used in my probabilistic model, I used an approach patterned after Lee and Rieman (1997), Peterson and Evans (2003), and Steventon et al. (2003). Using an external stochastic population model, I output a case file of model results, which I used to parameterize the nodes within the network. Model created case files are a database of findings including values for input parameters, intermediate variables, and output variables of interest (Steventon et al. 2003). Because parameter uncertainty works in concert with variability in biological systems, I used the combination of a large number of model runs to estimate probabilities of various population responses while accounting for uncertainty in the system. I conducted 500,000 simulations using random combinations of input parameter estimates that were representative of white-tailed deer in

¹ Paper was published posthumously by Richard Price.

Arkansas and across the U.S. (Tables 1 and 2). After simulating white-tailed deer population dynamics for a 20-year period, the resulting output at the 20th year was used to parameterize the CPT within the graphical structure.

Using this modeling approach, I evaluated the effect of white-tailed deer SHC on the residual (post-harvest) population age structure and residual (post-harvest) population sex ratio of white-tailed deer populations in Arkansas. I conducted sensitivity analysis to examine the influence of model parameters on residual population age structure and residual population age structure. I conducted sensitivity analysis on the graphical model nodes within NETICA. Sensitivity was expressed as the percent reduction in variance of the query variable (response variable of interest) given the specification (values) in the findings variables (variables conditionally related to the query variable) (B. Boerlage, Norsys Software Corp., personal communication). Because my interest was in evaluating the sensitivity of population responses to different management strategies and biological parameters at multiple scales, all sensitivity analysis was conducted in the models initialized state.

RESULTS

Model Assumptions

In those situations where female harvest data was unavailable for historical periods, age structure values used in modeling were based on information collected at the regional level, assuming that age structure of female harvest was equal between periods of regulation. I detected no difference in female age harvest structure between periods of historical and current regulations (0.0121 (SE=0.0125), $\chi^2_1=0.093$, P=0.3337).

Initialized Probabilistic Model

Horizontal bars (belief vectors) and their associated numerical values represent the probability that a given node is in a particular state. Uniformity in belief vectors indicated that the underlying population model selected those values are random from a uniform distribution. As an example, the belief vector structure for the node Abundance (Fig. 1) illustrates that in the probabilistic models initialized state, there was a wide range of belief regarding the state of Abundance, indicating uncertainty due to unknown values for hunting camp size and density. For continuous nodes, estimates for the mean abundance (expected value of the probability distribution and associated standard deviation) for the node are shown at the bottom of each node. For example, mean and standard deviation values for the node Abundance were shown at the bottom of the node ($\bar{x}=191 \pm 120$). In order to reduce the frequency of lines shown in the graphical structure, causal links (arrows) were overlapped (as shown by Haas 1992) (Figs. 3, 4), so single lines may carry more than one relationship.

Sensitivity Analysis

Local Model.—I present in Table 3 the sensitivity analysis at the local scale for model node residual sex ratio. The residual population sex ratio was most sensitive to pre-harvest sex ratio and initial population sex ratio. Knowledge of harvest sex ratio was less important, and the regulatory restrictions had no influence on reducing variation in residual sex ratio. Across each male age class, residual male age structure was most sensitive to population age structure prior to harvest (proportion of male population in each age class) (Table 4). Male harvest rate was somewhat important for predicting the residual male sub-adult population, less so for the adult population, and had no influence on residual male fawn or yearling population. Knowledge of the regulatory restrictions

and harvest data did not reduce uncertainty in predicting residual population age structure for all age classes.

Scale Model.—I present in Table 5 the sensitivity analysis for the scale model node residual sex ratio. Residual population sex ratio was most sensitive to pre-harvest sex ratio, but to a lesser extent than that shown in the local model (15% v. 77%). Knowledge of all other sex ratio predictive nodes explained <5% of total variation in the predictions of residual population sex ratio (Table 5). As with the local model, for each male age class residual male age structure was most sensitive to population age structure prior to harvest (proportion of male population in each age class) (Table 6). Male harvest rate was somewhat important for predicting the residual male fawn and yearling residual population, but was less useful for predicting sub-adult and adult residual population. Adult male residual population was most sensitive to pre-harvest population structure, and insensitive to all other input variables. For all male age classes, knowledge of the regulatory restrictions, county, or region reduced uncertainty in predicting residual population age structure <10%.

Benefits of Additional Information

Local Model-Probability density plots for residual male population structure at the local scale indicated small differences in residual population structure in response to the management restriction. Across all age classes, there were slight increases in the residual population age structure (Figs 5 and 6) indicating an increased probability of more male white-tailed deer, by age class, being recruited in to the residual population. Cumulative probabilities indicated that fawn and yearling residual populations met or exceeded 15% of the total population size in $\leq 12\%$ (historical) and $\leq 15\%$ (current) of simulated

responses to regulatory restrictions. Under historical regulations, residual population structure for both sub-adult and adult males exceeded 5% of total population size in $\leq 9\%$ and $\leq 17\%$ of simulated responses (cumulative probabilities of 0.91 and 0.73, respectively) and exceeded 10% of total population size in $\leq 4\%$ of simulated responses. Under current regulations, residual population structure exceeded 5% of the total population size in $\leq 10\%$ and $\leq 32\%$ and exceeded 10% of the total population in $\leq 5\%$ of simulated responses. Evaluation of residual female population structure indicated that there were no changes in age structure due to regulations.

Predicted average residual sex ratio (No. Males/No. Females) for periods of historical regulations was 0.36 (0.031), increasing during current regulations to 0.42 (0.037). Probability densities for predicted residual sex ratio at the local scale indicated that the regulatory restrictions caused a shift in residual sex ratio (Fig. 7). Residual sex ratio met or exceeded the commonly stated optimal level (0.5 or 1-male/2-females) in $\leq 11\%$ of simulated responses under historical regulations, and $\leq 19\%$ under current regulations.

Scale Model-Using conventional BBN logic, when an input node is completely specified (e.g. Region=LMAV) while other nodes are left unspecified (e.g. County; hence all counties within the LMAV are equally likely) (D. Steventon, B.C. Ministry of Forests, personal communication), when passing through the probabilistic structure provides the response probabilities for the residual population structure providing the probability of each response given the uncertainty as to which county within the LMAV is being addressed (Lee and Rieman 1997). The node sequence for the input harvest data was: Region –County –Harvest Data. Thus, I evaluated the male population response at 3

levels of node specification: (1) state level, where all regions and counties are equally likely, (2) regional level, where one region is completely specified (LMAV), and (3) county level (Arkansas County).

Probability density plots and cumulative distributions at the county level indicated a loss of predictive resolution due to aggregation at higher spatial scales. Cumulative probabilities for Arkansas Co. indicated that fawn populations exceeded 15% of total population size in $\leq 5\%$ (historical) and $\leq 12\%$ (current) of simulated responses to regulatory restrictions (Fig. 8). Under historical regulations, yearling males exceeded 10% of total population size in $\leq 1\%$ of predictions, but under current regulations, yearlings exceeded 10% of total population size in 30% of responses (Fig 8). Model predictions for Arkansas Co. indicated that residual sub-adults exceeded 10% of the total population size in $\leq 1\%$ under historical regulations, and never under current regulations (Fig. 9). Predicted responses for both periods of regulations indicated that male adults exceeded 10% of population size in $\leq 2\%$ of predictions for both regulatory periods (Fig 9.).

Male yearlings constituted a higher proportion of the residual population structure under current regulations at all spatial scales (Figs. 8, 10, and 12). Sub-adult and adult male residual population structure under current regulations exceeded those predictions under historical regulations with low probability (Figs. 9, 11, and 13). Model predictions indicated that for the scale model, residual population structure for sub-adult and adult males was lower under current regulations than historical regulations (Figs. 9, 11, and 13).

Model estimated mean (var) for residual sex ratio during periods of historical regulations in Arkansas Co. were 0.34 (0.014), increasing under current restrictions to 0.52 (0.04). Evaluation of residual sex ratio in Arkansas Co. indicated that under current restrictions, optimal sex ratio was reached in $\leq 32\%$ of predictions, while under historical regulations; it was met in $\leq 4\%$ of predictions. At lower spatial resolution under historical regulations, mean model estimated residual sex ratio was 0.33 (0.02) and 0.33 (0.02) for the LMAV and across Arkansas, respectively (Fig. 14). Under current regulations, these estimates shifted towards optimal levels (0.40 (0.04) and 0.48 (0.05), respectively), but with increasing variance. Optimal sex ratio was met in $\leq 5\%$ of predictions under historical regulations for both the LMAV and across Arkansas. Under current regulations, optimal sex ratio was met in $\leq 43\%$ and $\leq 35\%$ of model predictions for the LMAV and across Arkansas, respectively.

DISCUSSION

Modeling approaches that accurately depict population patterns at multiple scales represent a challenge for wildlife managers (Borsuk et al. 2004). While use of population models has become common for most wildlife species (White and Lubow 2002), sufficient data to evaluate model structure and test underlying assumptions regarding relationships between population parameters and harvest is unavailable at many scales. Uncertainty associated with model parameters due to demographic and process variation and the form which the population model takes limits manager's ability to predict future states (Lee and Rieman 1997, Lee 2002). By representing the stochastic population model in a probabilistically based graphical form, researchers can clearly illustrate uncertainty associated with population parameters, the causal relationships between these

parameters, and how updated information can influence response predictions. My approach should not be viewed as a substitute for rigorous empirical evaluation of white-tailed deer populations, but as a management tool to be used with continuously updated empirical data to evaluate plausible changes in population structure. As most white-tailed deer management planning takes place annually, my probabilistic model encompassed those factors which could be collected on an annual basis. The model I described here was developed to provide a realistic representation of the current knowledge about this system (Borsuk et al. 2004). While applications of graphical models and Bayesian statistics have been limited in ecology (Dennis 1996, Dixon and Ellison 1996, Peterson and Evans 2003), this approach allows managers to use explicit, quantitative methods to evaluate the impact of uncertainty and assist with directing research to gather additional information for management purposes (Lee and Rieman 1997, Haas 2001, Peterson and Evans 2003).

Limited availability of population specific parameter estimates contributes to prediction uncertainty (Lee and Rieman 1997), which is often overlooked by agencies during management planning and evaluation. While use of parameter estimates from rigorous studies is preferred when modeling population dynamics (McCallum 2000, Williams et al. 2002) frequently relevant data is limited, thus several population parameter ranges were constructed subjectively in my modeling approach. Although Coulson et al. (1999) feel that there is a “general paucity of work on small-scale spatial dynamics within populations” (Coulson et al. 1999, pp. 667), I propose that small-scale evaluations of harvest impacts on white-tailed deer population processes are the norm (McCullough 1979, Dusek et al. 1989, Fuller 1990, Beier and McCullough 1990,

Jacobson 1992), while large scale population dynamics studies are limited (McShea et al. 1997). Thus, management decisions implemented across multiple scales are untested and based on questionable ecological relationships. While abundance estimates are needed to construct adequate management programs to manipulate deer populations (MacNab 1985), little effort has been allocated to this purpose (Healy et al. 1997). Limited information on ecological processes shaping deer-habitat relationships combined with inadequate abundance information reduced my ability to specify process-based relationships for model abundance estimates. To avoid stationarity of landscape level processes (Fortin et al. 2003), habitat based abundance estimates were variable for each model realization. Although this approach is less optimal than county level abundance estimates, long-term landscape level experiments monitoring abundance are uncommon (McShea et al. 1997) as is information on deer-landscape relationships (Risenhoover et al. 1997, Healy et al. 1997). Based on these considerations, the estimates I used provide a viable range of per/county abundance based on underlying landscape characteristics and as such are justified. However, relationships between abundance and habitat structure may exist at different scales (Healy et al. 1997). My evaluation of harvest management impacts at multiple scales was based on the arbitrary resolution of county level information. Although county and regional designations in Arkansas are levels at which harvest data interpretations and management planning is conducted, they may not be equivalent to biological regions. Analysis at the level of deer management zone would be preferable; however, management zones in Arkansas were constantly in flux over the past decade. Thus, there is a loss of spatial resolution due to the lumping of data within counties that could conceal finer scale relationships between population parameters.

Survival rates were considered equal across sexes within age classes and were based on a range of values from scientific literature. However, recent work reported variation in survival rates between age-sex combinations of sheep (Jorgenson et al. 1997, Catchpole et al. 2000), red deer (Catchpole et al. 2004), and across age classes in white-tailed deer (Ditchkoff et al. 2001) which might be included in future model approaches.

Fryxell et al. (1991) concluded that frequent changes in management practices to reverse short-term trends in harvest success or population size may cause greater fluctuations in abundance than a constant harvesting policy. Based on my simulation model, I suggest that evaluation of regulatory impacts should be based on a minimum of 5 years of experimental data. Due to the stochastic nature of populations in variable environments, more time might be needed to address variance components when attempting to identify population trends (see Thompson et al. 1998).

Similarity of response profiles for males under both restriction levels could be due to hunter selectivity (McCullough 1979) and the current SHC's inability to differentiate between males in these age classes based on antler characteristics (Roseberry and Klimstra 1975). Higher levels of residual population structure for adult males than sub-adults is most likely due to a broader range of harvest frequencies for the sub-adult age class and equivalent initial distributions for both classes. Although harvest rates are often specified in simulation modeling exercises for white-tailed deer in place of harvest data (Bender and Roloff 1996, Xie et al. 1999), limited knowledge of population size, structure, harvest rate, and how these parameters interact across the range of white-tailed deer has restricted their use in models for regulatory planning. This forces managers to evaluate harvest statistics using ad hoc approaches (Roseberry and Woolf 1991,

McCullough et al. 1990) that do not account for demographic or process variation in the modeling procedures (Lubow et al. 1996).

Based on my modeling results for current regulations at the local scale, population response profiles for sub-adult and adult males were higher than when under historical regulations. However, as scale increased, population responses under current regulations tended to decline to levels below those under historical regulations. Cumulative probability distributions for current regulations indicated that while yearling male residual populations show considerable response to current regulations, this response was negated after age class transition due to high levels of sub-adult harvest. It was my expectation that regulatory restrictions would reduce yearling harvest, hence increasing their frequency in the residual population. My results indicated that those shifts were cancelled out by increased selectivity of sub-adults under current regulations (and possibly high quality yearlings), allowing no more males to reach mature (≥ 3.5 year old) age classes than under historical regulations. This agrees with results found by Hernbrode (1987), Bender and Miller (1999), and previous suggestions made by Carpenter and Gill (1987) and Shea et al. (1992). Adult male population response varied little at larger scales and as spatial resolution declined the response probability distributions tended to converge. I propose this result was a combination of declining influence of antler restrictions and uncertainty due to parameter estimates and model structure.

The current belief among deer biologists is that population structure, trajectory, and management evaluations can all be conducted using harvest data (Hayne 1984, Roseberry and Woolf 1991, McCullough et al. 1990). But, my results indicate that

information concerning vital rates and population status (Lubow et al. 1996) as well as harvest rates is necessary for adequate population management. Although, there was still uncertainty associated with belief vectors for male population response after additional information was incorporated on regulatory restrictions, increased specification using updated empirical data could increase our degree of belief in certain population responses. I found that knowledge of pre-harvest population structure was most important for predicting population response. However, limited effort has been applied by managers to gather pre-harvest population structure, as it is both logistically and monetarily expensive. Residual population structure was also influenced by harvest rate, more so for fawns and yearlings at higher scales, sub-adults and adults at the local scale.

Residual sex ratio is considered a management parameter of interest by most ungulate biologists (Demarais et al. 2000, but see White et al 2001) and is assumed to affect recruitment rates (Jacobson 1992), breeding synchrony (Gruver et al. 1984, Guynn et al, 1988, Jacobson 1992), fetal sex ratio (Verme 1981), and survival rates (Rutberg 1987, Miller and Ozoga 1997). Conclusions regarding residual population sex ratio are usually based on harvest data through correlative studies (Jacobson 1992) and the impact of population sex ratio on breeding success has currently not been experimentally evaluated (White et al. 2001). Sensitivity results from my study indicate that residual population sex ratio was most sensitive to pre-harvest sex ratio and initial population sex ratio. As neither pre-harvest sex ratio nor initial population sex ratio are commonly estimated from field data for use in population models, biologists typically use the assumption of equal population sex ratio (Jenks et al. 2002, Phillips and White 2003) or by basing sex ratio on harvest information (McCullough 1990, Xie et al. 1999). My

results however imply that information on pre-harvest sex ratio, possibly collected by archery hunters, could increase precision (77% reduction in uncertainty at local scale) when forecasting residual sex ratio. Harvest sex ratio had limited influence on predicting residual population sex ratio ($\leq 10\%$ at all scales).

Different approaches to ecological modeling attempt to combine information from multiple studies into predictive relationships for management purposes (Jorgenson 1993). Although there have been an increasing number of studies estimating white-tailed deer population parameters, the usefulness of parameter estimates from these studies is artificial until they are incorporated into population models. Extensive variability exists in population parameter estimates for white-tailed deer and information regarding population parameters under different regulatory practices is not available. My approach explicitly represents this uncertainty and its impact on predictive ability. While management actions for white-tailed deer are intended to manipulate population characteristics (Demarais et al. 2000), limited demographic information on population parameters has required most management planning to use information collected from harvested deer (Roseberry and Woolf 1991). Modeling processes used to plan and evaluate white-tailed deer management actions often do not explicitly account for uncertainty in parameter estimates, often using estimates with exaggerated precision (Lee 2002) hindering management effectiveness.

MANAGEMENT IMPLICATIONS

One of the primary benefits of the graphical modeling approach is that this approach allows managers to incorporate additional information simply by refining degree of belief in each node, which then updates model probabilities. This limits the need for continuous

model re-evaluation, which would be necessary as additional information becomes available (see Alpizar-Jara et al. 2001 for a different approach). Because population parameters were constructed to encompass a viable range of vital rates, population responses can be examined across a range of parameter values.

Based on the results from my study, I suggest the managers begin implementation of white-tailed deer adaptive management programs (McShea et al. 1997, Williams 1997). I encourage white-tailed deer managers to broaden or redirect data collection efforts to include annual estimation of population size and structure and estimation of harvest rates. Although it is expensive and difficult for wildlife managers to gather reliable knowledge across large spatial scales (McShea et al. 1997), as the public involvement in white-tailed deer management increases (Demarais et al. 2000) incorporation of multiple management practices and rigorous evaluation of uncertainty in population modeling scenarios will become increasingly important parts of the regulatory decision making process. In addition, I suggest that concurrent experimental studies at multiple spatial scales are in order to evaluate population parameter relationships (McShea et al. 1997, White and Lubow 2002). Future evaluations of population parameter relationships under different harvest management programs across multiple spatial and temporal scales can increase parameter certainty and as such increase the accuracy of the decision process.

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TABLES

Table 1. Stochastic age- and sex-structured population simulation model parameters for local model, parameter definitions and data sources, distributional form used for selection, and estimated range of values.

Parameter	Parameter Definition and Data Source	Distribution	Estimated Value (Range)										
Density	White-tailed deer density (ha) on Deer Camp Program (DCP) properties in Arkansas. AGFC Expert Opinion.	Uniform	Min: 0.15 Max: 0.50										
Camp Size	Size (ha) of DCP properties in Arkansas. Range of values was estimated from results of DCP survey across Arkansas	Uniform	Min: 80 Max: 1100										
Sex Ratio	Population sex ratio (males:females). Range of values was determined from AGFC herd composition counts and AGFC expert opinion.	Uniform	Min: 0.1 Max: 0.5										
Age Structure	Population age structure (expressed in % by age and sex). Expected values estimated from AGFC recruitment study (females) and expert opinion (males).	Dirichlet	<table border="0"> <tr> <td><u>Males</u></td> <td><u>Females</u></td> </tr> <tr> <td>Fawn=0.40</td> <td>Fawn=0.175</td> </tr> <tr> <td>Yearling=0.30</td> <td>Yearling=0.175</td> </tr> <tr> <td>SubAdult=0.15</td> <td>SubAdult=0.25</td> </tr> <tr> <td>Adult=0.15</td> <td>Adult=0.40</td> </tr> </table>	<u>Males</u>	<u>Females</u>	Fawn=0.40	Fawn=0.175	Yearling=0.30	Yearling=0.175	SubAdult=0.15	SubAdult=0.25	Adult=0.15	Adult=0.40
<u>Males</u>	<u>Females</u>												
Fawn=0.40	Fawn=0.175												
Yearling=0.30	Yearling=0.175												
SubAdult=0.15	SubAdult=0.25												
Adult=0.15	Adult=0.40												
Survival	Age specific natural survival rates for winter-spring-summer period. Values were estimated from literature and AGFC expert opinion and were constructed to cover the range of period survival rates of white-tailed deer across their range.	Uniform	Fawn: Min: 0.3, Max: 0.99 Yearling: Min: 0.3, Max: 0.99 SubAdult: Min: 0.7, Max: 0.99 Adult: Min: 0.7, Max: 0.99										
Recruitment	Average juvenile recruitment rate of female white-tailed deer for each age class. Mean values were estimated from AGFC recruitment study.	Poisson	Fawn: 0.03 Yearling: 1.22 SubAdult: 1.69 Adult: 1.78										
Juvenile Survival	Juvenile survival rates for the period from birth until recruitment into the fall fawn age class. Range of values estimated from literature and AGFC expert opinion.	Uniform	Min: 0.115 Max: 0.85										
Juvenile Sex Ratio	Sex ratio of juveniles at recruitment into the fawn age class. Range of values estimated from the literature and was event dependent (see text).	Uniform	Event: Min: 0.5 Event: Max: 0.65 No Event: Min: 0.30 No Event: Max: 0.5										
Event	Probability of a stochastic environmental event that causes a reduction in juvenile survival and a shift in juvenile sex ratios at recruitment (see	Bernoulli	P(Event)= 0.1										

text).

Harvest	Biological data collected from harvested individuals (classified by sex and age). Proportion harvested by sex and age represents the maximum likelihood estimate for each level of Scenario (see below).	Dirichlet	Dir (F, Y, S, A)
Harvest Rate	Rate multiplier used to reconcile biological data collected for each age-scenario combination. Ranges were based on AGFC expert opinion for 4 groups consisting of 3 scenarios and are age specific.	Uniform	<u>Group 1:</u> F-Y: Min: 0.25, Max: 0.75 S-A: Min: 1.00, Max: 2.00 <u>Group 2:</u> F-Y: Min: 0.50, Max: 1.50 S-A: Min: 1.00, Max: 2.00 <u>Group 3:</u> F-Y: Min: 0.25, Max: 1.25 S-A: Min: 1.00, Max: 2.00 <u>Group 4:</u> F-Y: Min: 0.75, Max: 2.00 S-A: Min: 1.00, Max: 3.00
Scenario	Different management scenarios representing combinations of regulatory restriction, property type, and localized management specific to biological data collected from DCP properties, which was used to estimate harvest parameters.	Scenario	1: Yes-Camp-Yes 2: Yes-Lease-Yes 3: Yes-Industry-Yes 4: Yes-Camp-No 5: Yes-Lease-No 6: Yes-Industry-No 7: No-Camp-Yes 8: No-Lease-Yes 9: No-Industry-Yes 10: No-Camp-No 11: No-Lease-No 12: No-Industry-No

Table 2. Stochastic age- and sex-structured population simulation model parameters for scale model, parameter definitions and data sources, distributional form used for selection, and estimated range of values.

Model Parameter	Parameter Definition and Data Source	Distribution	Estimated Value (Range)										
Density	White-tailed deer density (km ²) estimates for counties within an Arkansas region. AGFC Expert Opinion.	Poisson	Ozarks = 5 Ouachitas = 7 LMAV = 3 GCP = 10										
Sex Ratio	Population sex ratio (males:females). Range of values was determined from AGFC herd composition counts and AGFC expert opinion.	Uniform	Min: 0.1 Max: 0.5										
Age Structure	Population age structure (expressed in % by age and sex). Expected values estimated from AGFC recruitment study (females) and expert opinion (males).	Dirichlet	<table border="0"> <tr> <td><u>Males</u></td> <td><u>Females</u></td> </tr> <tr> <td>Fawn=0.50</td> <td>Fawn=0.125</td> </tr> <tr> <td>Yearling=0.30</td> <td>Yearling=0.125</td> </tr> <tr> <td>SubAdult=0.15</td> <td>SubAdult=0.25</td> </tr> <tr> <td>Adult=0.05</td> <td>Adult=0.50</td> </tr> </table>	<u>Males</u>	<u>Females</u>	Fawn=0.50	Fawn=0.125	Yearling=0.30	Yearling=0.125	SubAdult=0.15	SubAdult=0.25	Adult=0.05	Adult=0.50
<u>Males</u>	<u>Females</u>												
Fawn=0.50	Fawn=0.125												
Yearling=0.30	Yearling=0.125												
SubAdult=0.15	SubAdult=0.25												
Adult=0.05	Adult=0.50												
Survival	Age specific natural survival rates for winter-spring-summer period. Values were estimated from literature and AGFC expert opinion and were constructed to cover the range of period survival rates of white-tailed deer across their range.	Uniform	Fawn: Min: 0.3, Max: 0.99 Yearling: Min: 0.3, Max: 0.99 SubAdult: Min: 0.7, Max: 0.99 Adult: Min: 0.7, Max: 0.99										
Recruitment	Average juvenile recruitment rate of female white-tailed deer for each age class. Mean values were estimated from AGFC recruitment study.	Poisson	<u>Ozarks</u> Fawn: 0.0 Yearling: 0.83 Sub-Adult: 1.92 Adult: 1.86 <u>Ouachitas</u> Fawn: 0.0 Yearling: 1.11 SubAdult: 1.4 Adult: 1.54 <u>LMAV</u> Fawn: 0.05 Yearling: 0.82 Sub-Adult: 1.53 Adult: 1.78 <u>GCP</u> Fawn: 0.0 Yearling: 1.58 Sub-Adult: 1.12 Adult: 1.69										

Juvenile Survival	Juvenile survival rates for the period from birth until recruitment into the fall fawn age class. Mean value estimated from literature and AGFC expert opinion.	Normal	Mean =0.5(SE=0.1)
Juvenile Sex Ratio	Sex ratio of juveniles at recruitment into the fawn age class. Range of values estimated from the literature and was event dependent (see text).	Uniform	Event: Min: 0.5 Event: Max: 0.65 No Event: Min: 0.30 No Event: Max: 0.5
Event	Probability of a stochastic environmental event that causes a reduction in juvenile survival and a shift in juvenile sex ratios at recruitment (see text).	Bernoulli	P(Event)= 0.1
Harvest	Biological data collected from harvested individuals (classified by sex and age). Proportion harvested by sex and age represents the maximum likelihood estimate for each age-sex-regulation combination.	Dirichlet	Dir (F, Y, S, A)
Harvest Rate	Rate multiplier used to reconcile biological data collected for each age-regulatory combination. Ranges were based on AGFC expert opinion for both sexes for both periods of regulatory restrictions.	Uniform	<u>Males (Historical Regs):</u> F-Y: Min: 0.75, Max: 2.00 S-A: Min: 1.00, Max: 2.00 <u>Females (Historical Regs):</u> F-Y: Min: 0.25, Max: 1.00 S-A: Min: 0.50, Max: 1.00 <u>Males (Current Regs):</u> F-Y: Min: 0.25, Max: 1.25 S-A: Min: 1.00, Max: 2.00 <u>Females (Current Regs):</u> F-Y: Min: 0.50, Max: 1.50 S-A: Min: 1.00, Max: 2.00
Poach	Ancillary loss rate representing losses from poaching and wounding loss	Uniform	F-Y: Min: 0.00, Max: 0.15 S-A: Min: 0.00, Max: 0.30

Table 3. Variance reduction (%) for white-tailed deer residual population sex ratio for the local model based on initialized model conditional probabilities and the values of the parent nodes.

Influence Node	Variance Reduction (%)
Pre-Harvest Sex Ratio	77.7
Initial Population Sex Ratio	58.3
Harvest Sex Ratio	10.7
Regulations	<1

Table 4. Variance reduction (%) of male white-tailed deer residual age structure for the local model based on initialized model conditional probabilities and the values of the parent nodes.

Influence Node	<u>Age Class</u>			
	Male Fawn	Male Yearling	Male Sub-Adult	Male Adult
Pre-Harvest Population	72.5	78.6	47.2	60.1
Harvest Rate	1.2	1.3	17.4	8.9
Regulatory Structure	<1	<1	2.2	1.4
Harvest Data	<1	<1	<1	<1

Table 5. Variance reduction (%) for white-tailed deer residual population sex ratio for the scale model based on initialized model conditional probabilities and the values of the parent nodes.

Influence Node	Variance Reduction (%)
Pre-Harvest Sex Ratio	15.1
Initial Population Sex Ratio	4.1
Harvest Sex Ratio	3.8
Regulations	1.2

Table 6. Variance reduction (%) of male white-tailed deer residual age structure for the scale model based on initialized model conditional probabilities and the values of the parent nodes.

Influence Node	<u>Age Class</u>			
	Male Fawn	Male Yearling	Male Sub-Adult	Male Adult
Pre-Harvest Population	37.3	38.2	42.3	71.8
Harvest Rate	11.1	11.1	1.7	<1
Regulatory Structure	8.6	9.5	2.9	<1
County	6.4	3.2	3.7	<1
Region	<1	<1	<1	<1

FIGURES

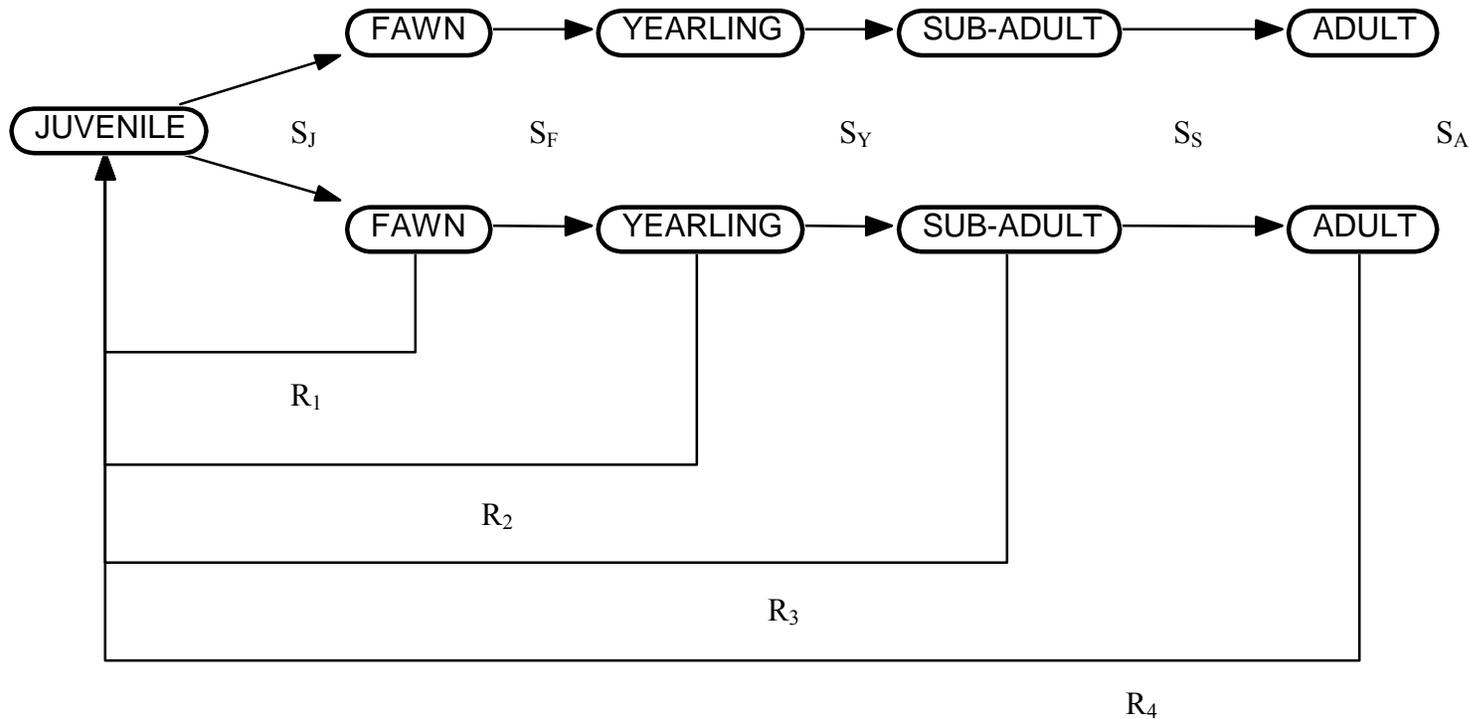


Fig. 1. Transition structure based on natural survival rates for the stochastic age- and sex-structured white-tailed deer population model. Stages Juvenile, Fawn, Yearling, Sub-Adult, and Adult represent spring births, 6 month old, 1.5 year old, 2.5 year old, and 3.5 year old, respectively. Survival rates (S) represent the survival rates for periods 1) summer until recruitment into Fawn class for Juveniles, and 2) winter, spring, summer for all other age classes until transitioning into next age class (where adults transition within the adult class). Recruitment rates (R_i) represent reproductive rates (mean No. fetuses) for each female age class.

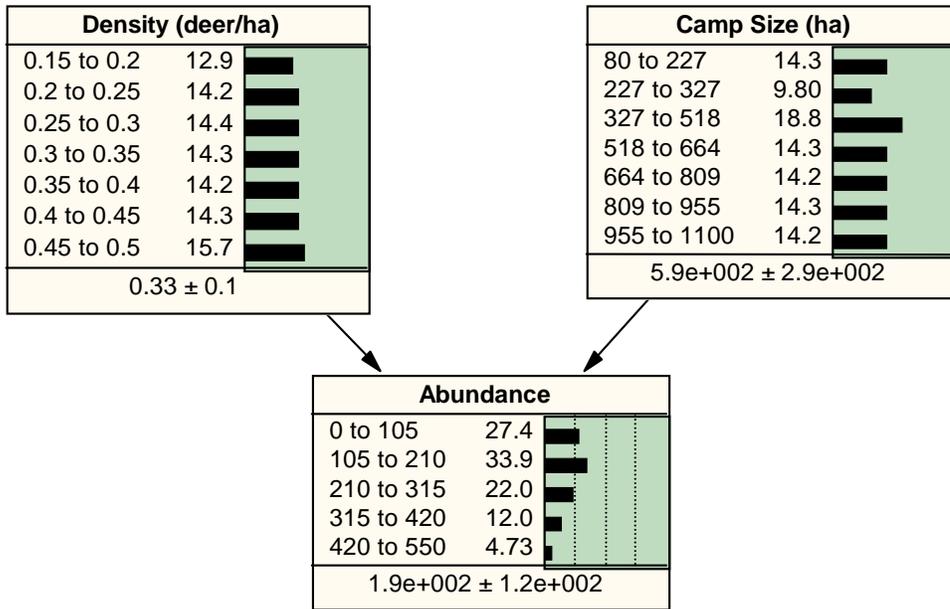


Figure 2. Probabilistic network in its initialized state based on output from simulation model for estimating white-tailed deer abundance on hunting camps registered in the Arkansas Deer Camp Program (DCP). Values associated with the bars in each histogram represent the probabilities of the node being in a particular stat

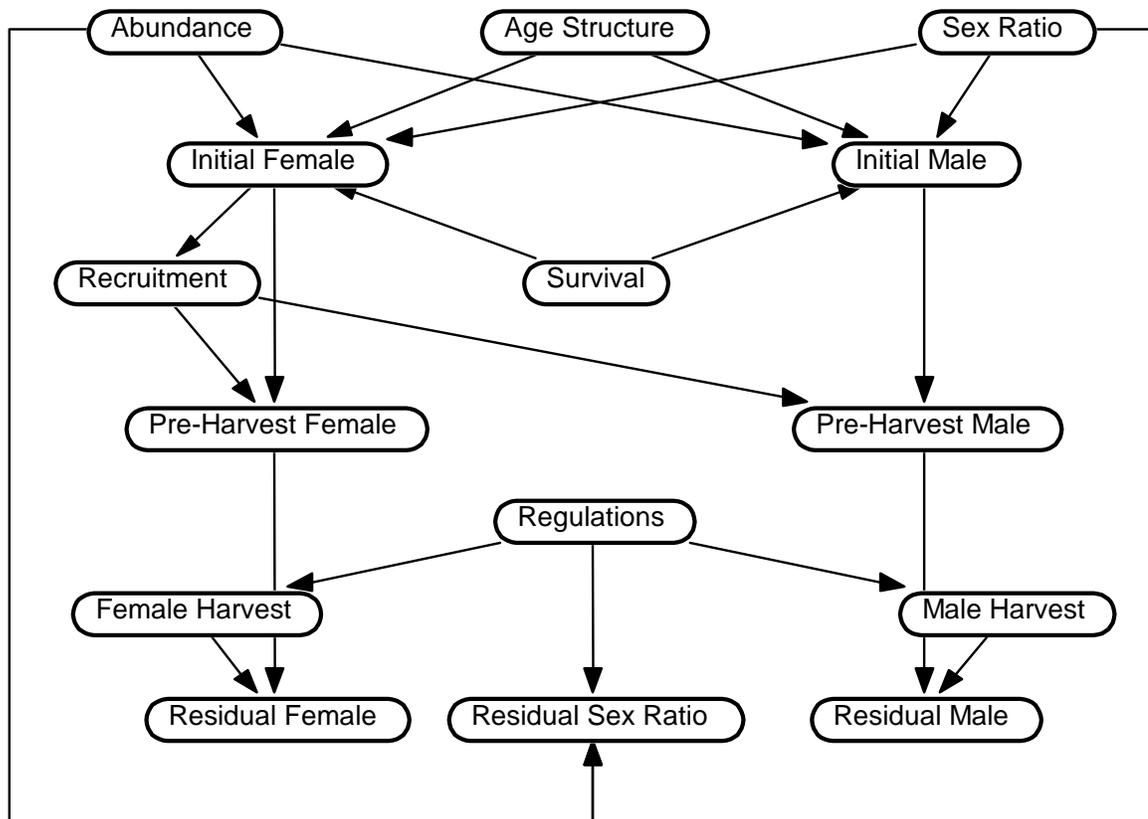


Fig. 3. A graphical representation of Arkansas local scale white-tailed deer probabilistic model showing the primary node groups used in the model. Model parameters, definitions, and values are shown in Table 1. Nodes for evaluation of each sex, survival, and harvest were modeled separately for fawns, yearlings, sub-adults, and adults, but are represented by a single node to simplify understanding.

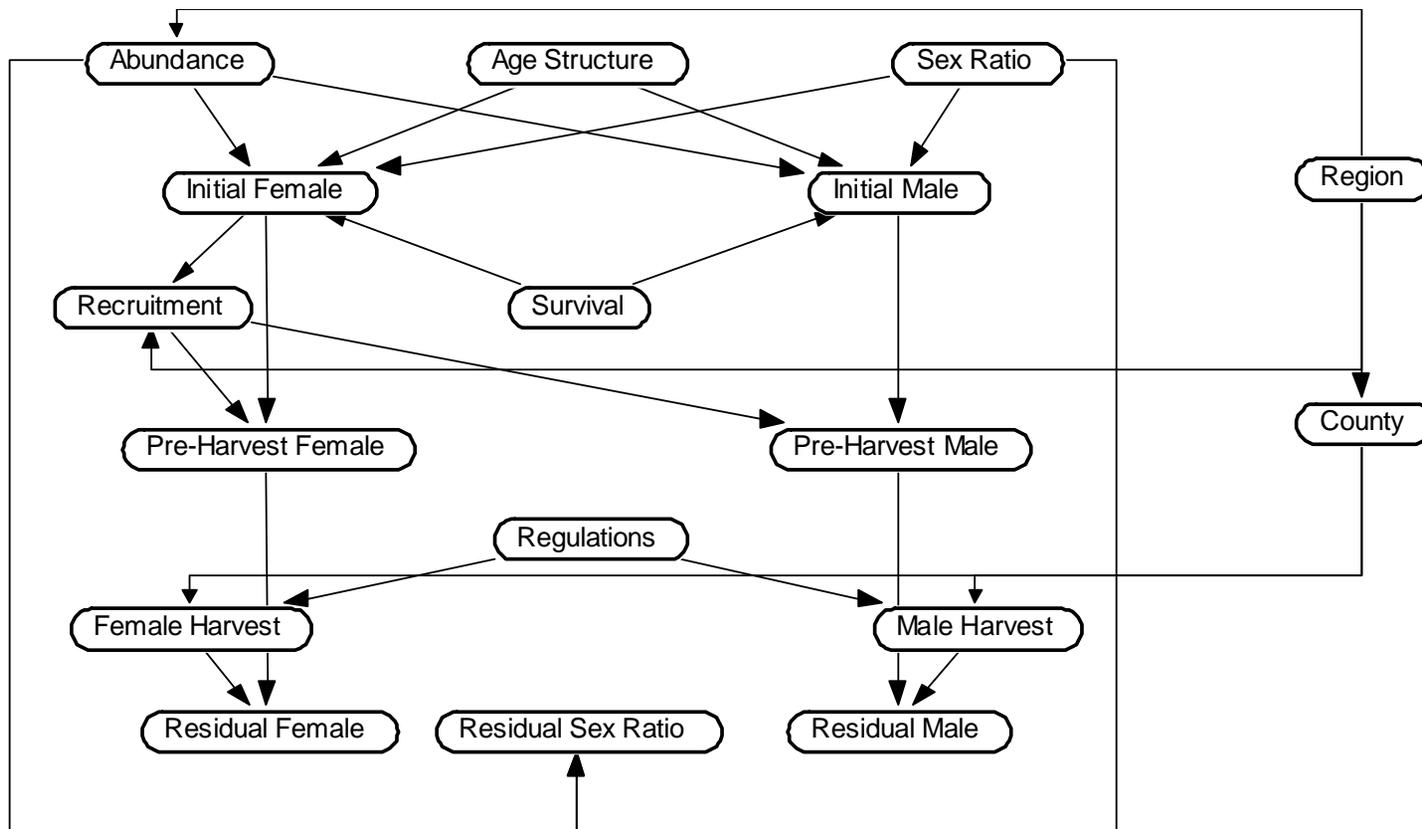


Fig. 4. Simple representation of Arkansas white-tailed deer scale probabilistic model. Model parameters, definitions, and values are shown in Table 1. Nodes for evaluation of each sex, survival, recruitment, harvest, and population structure were modeled separately for fawns, yearlings, sub-adults, and adults but are represented by a single node to simplify understanding.

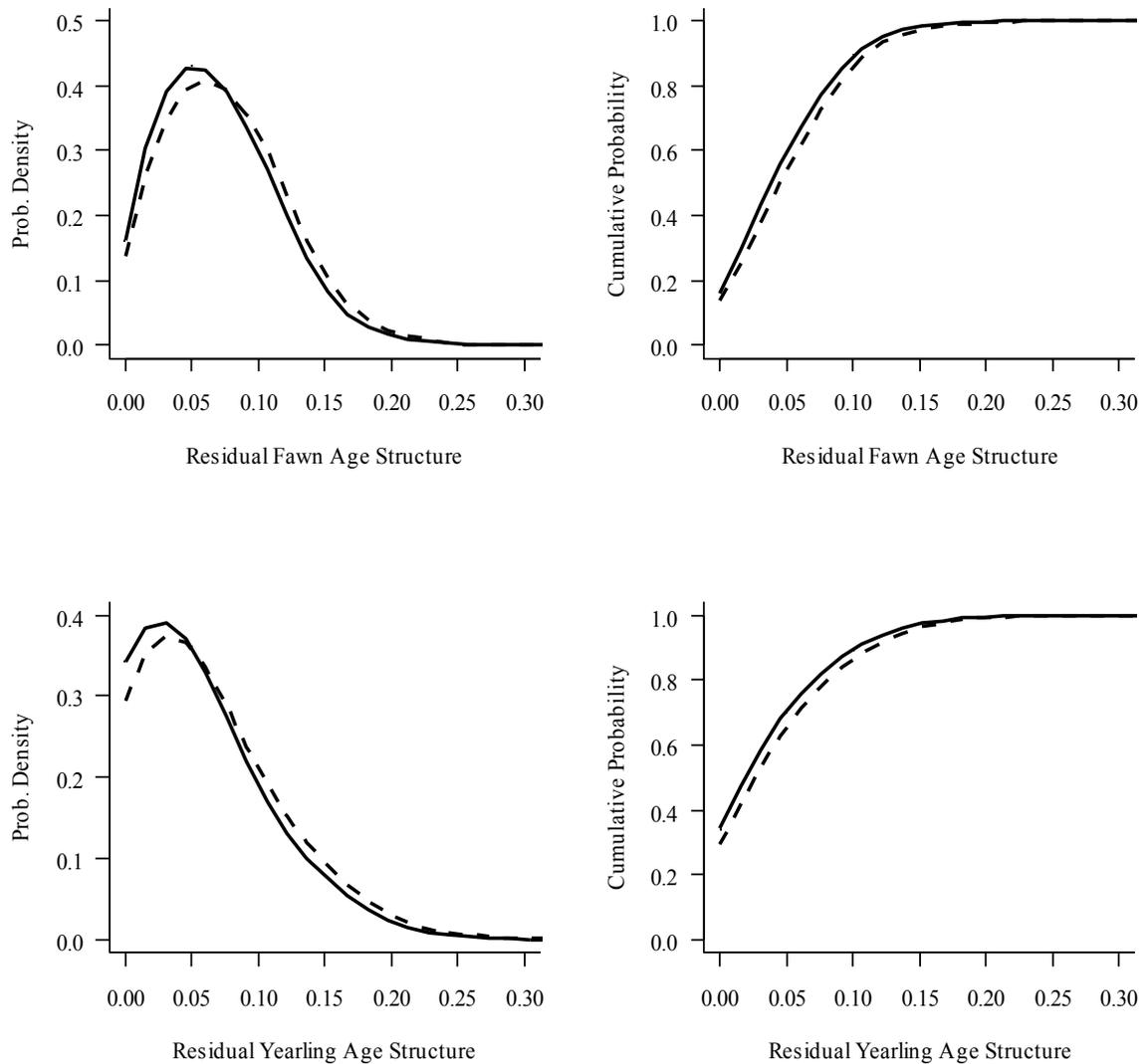


Fig. 5. Predicted probability density and cumulative probability distributions for fawn and yearling male white-tailed deer residual age structure modeled at the local scale for 2 periods of regulatory restrictions (expressed as a proportion of total population). The historical scenario (no antler restriction) is shown as a solid line, and the management scenario (antler restriction) currently in use in Arkansas is shown as a dashed line.

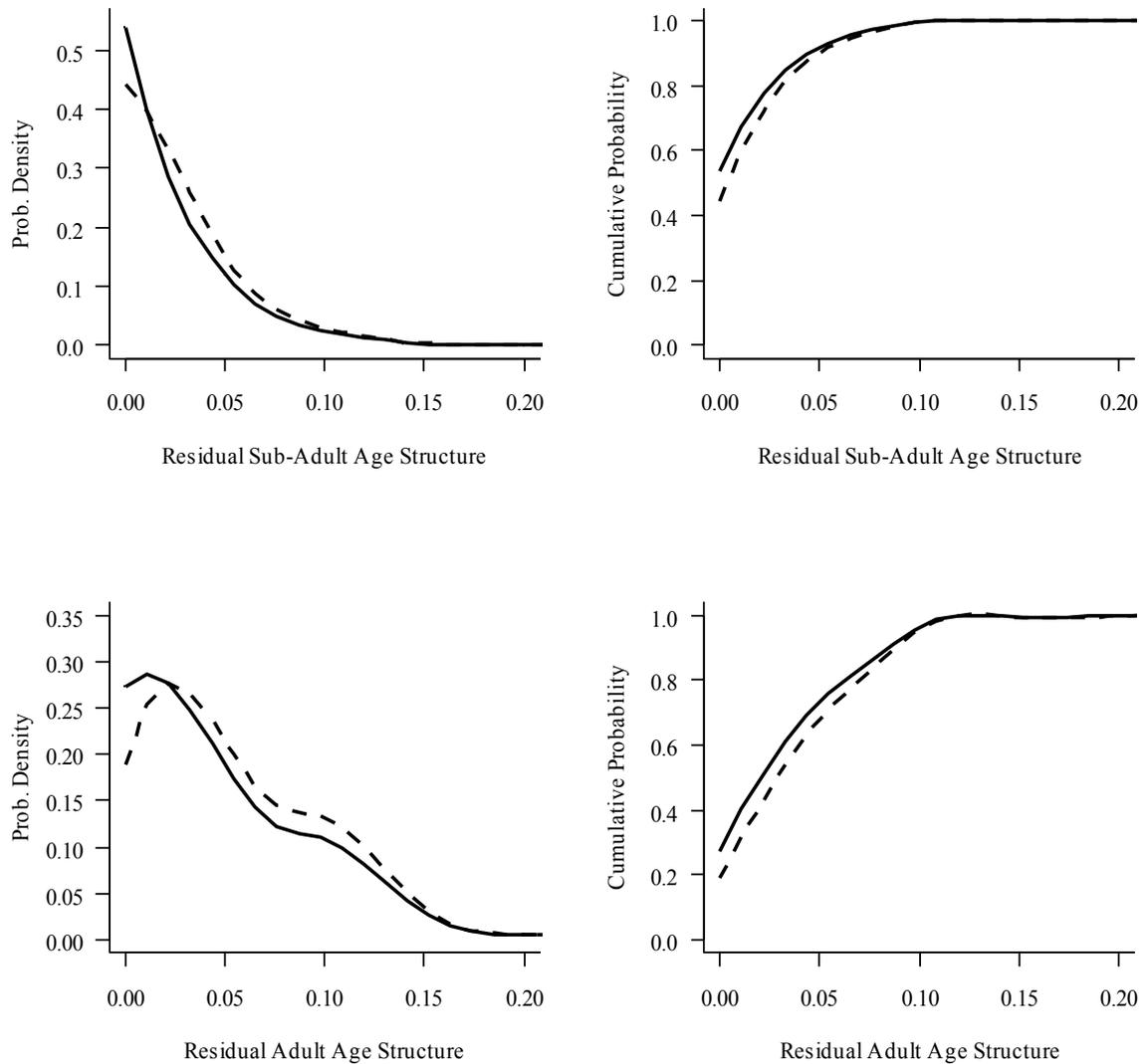


Fig. 6. Predicted probability density and cumulative probability distributions for sub-adult and adult male white-tailed deer residual age structure modeled at the local scale for 2 periods of regulatory restrictions (expressed as a proportion of total population). The historical scenario (no antler restriction) is shown as a solid line, and the management scenario (antler restriction) currently in use in Arkansas is shown as a dashed line.

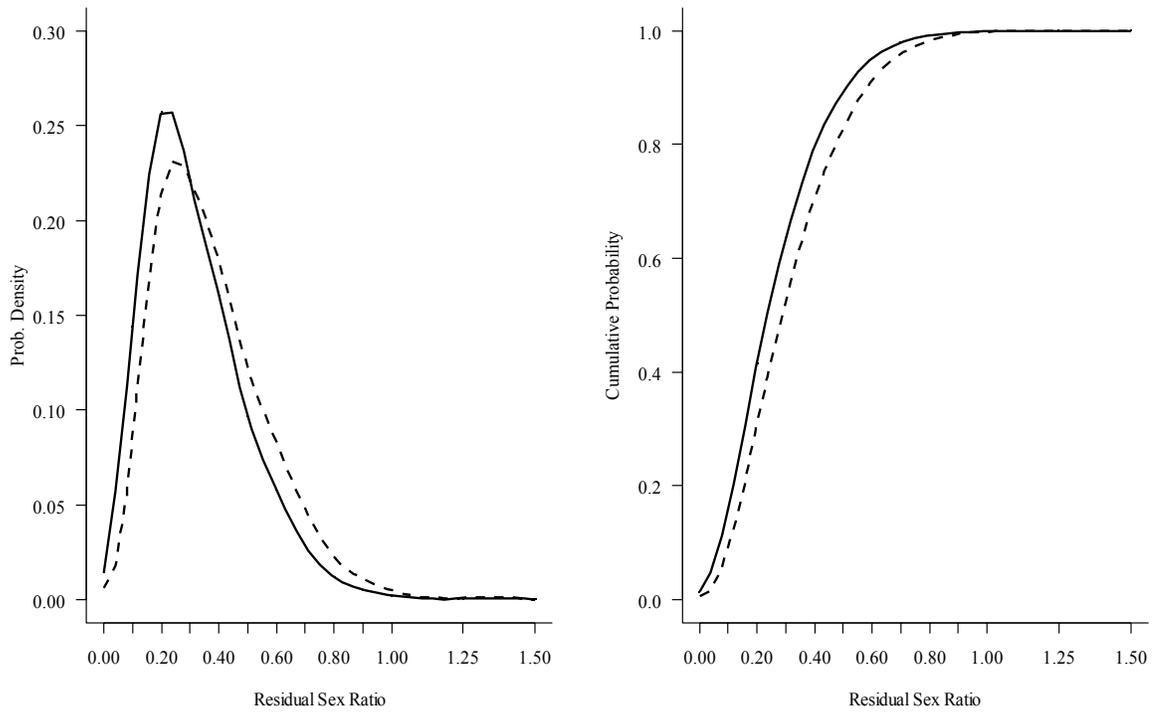


Fig. 7. Predicted probability density and cumulative probability distributions for residual population sex ratio modeled at the local scale for 2 periods of regulatory restrictions (expressed as No. Males/No. Females). The historical scenario (no antler restriction) is shown as a solid line, and the management scenario (antler restriction) currently in use in Arkansas is shown as a dashed line.

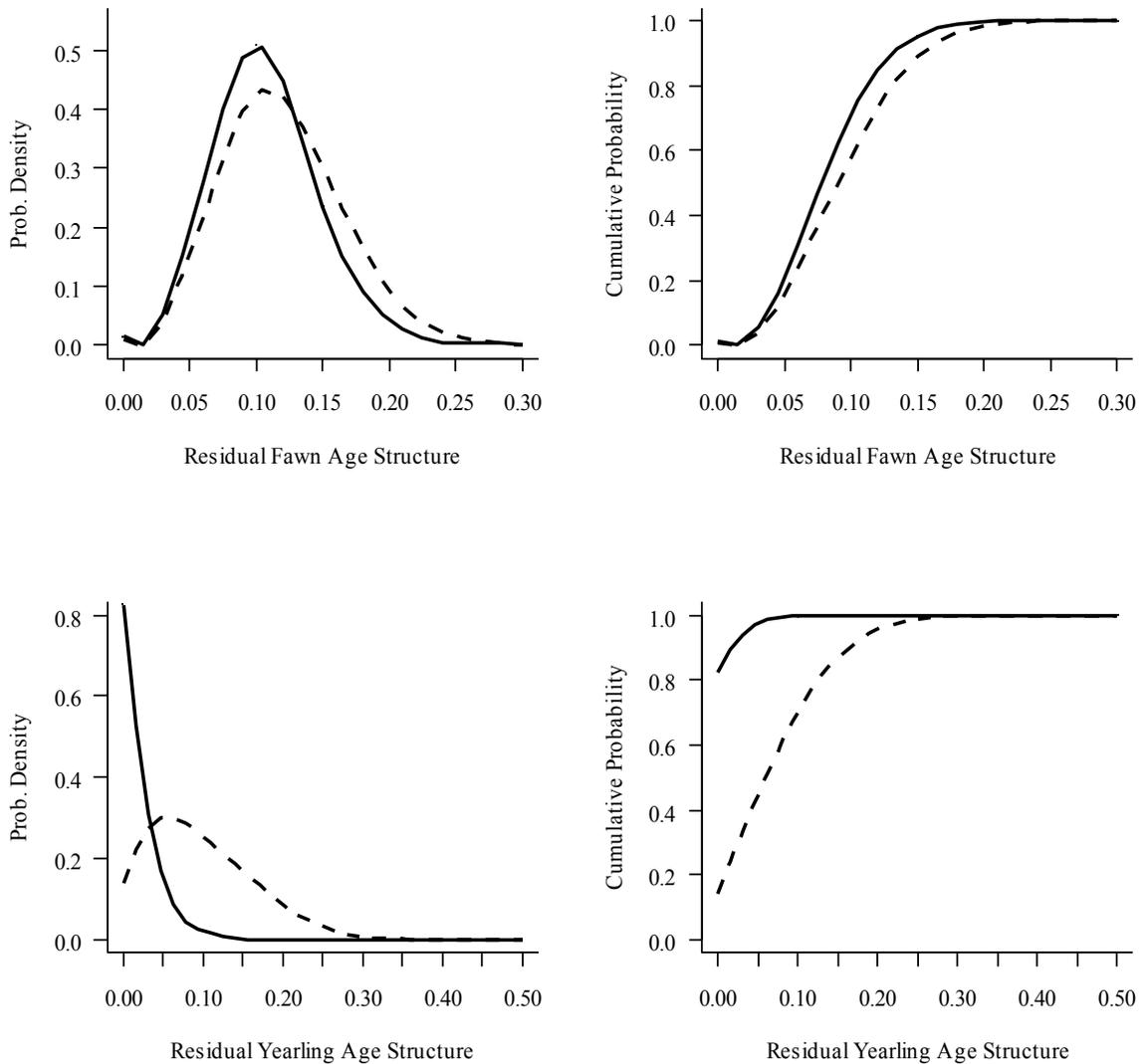


Fig. 8. Predicted probability density and cumulative probability distributions for fawn and yearling male white-tailed deer residual age structure for 2 periods of regulatory restrictions modeled at the county level (Arkansas Co.) (expressed as a proportion of total population). The historical scenario (no antler restriction) is shown as a solid line, and the management scenario (antler restriction) currently in use in Arkansas is shown as a dashed line.

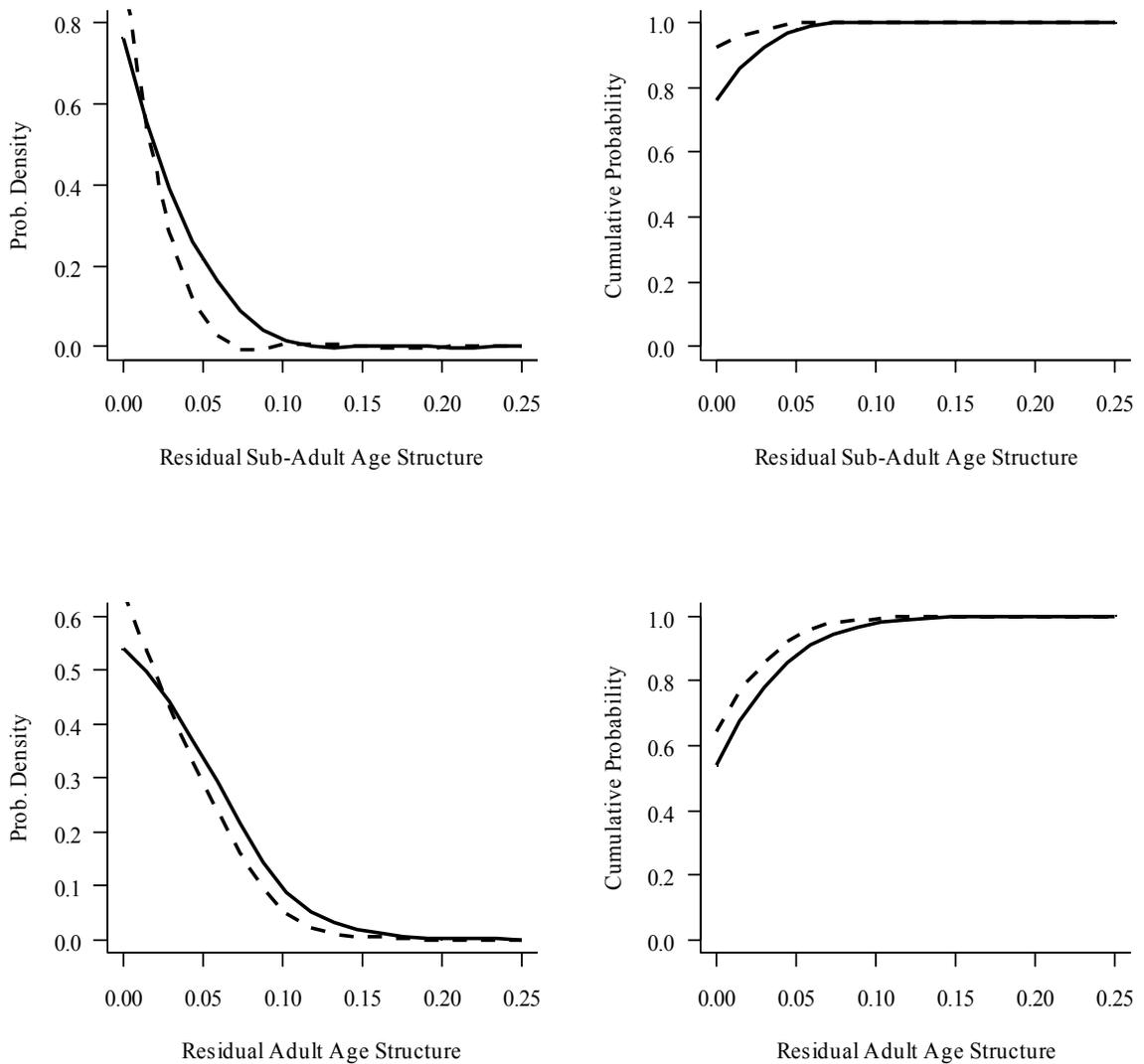


Fig. 9. Predicted probability density and cumulative probability distributions for sub-adult and adult male white-tailed deer residual age structure for 2 periods of regulatory restrictions modeled at the county level (Arkansas Co.) (expressed as a proportion of total population. The historical scenario (no antler restriction) is shown as a solid line, and the management scenario (antler restriction) currently in use in Arkansas is shown as a dashed line.

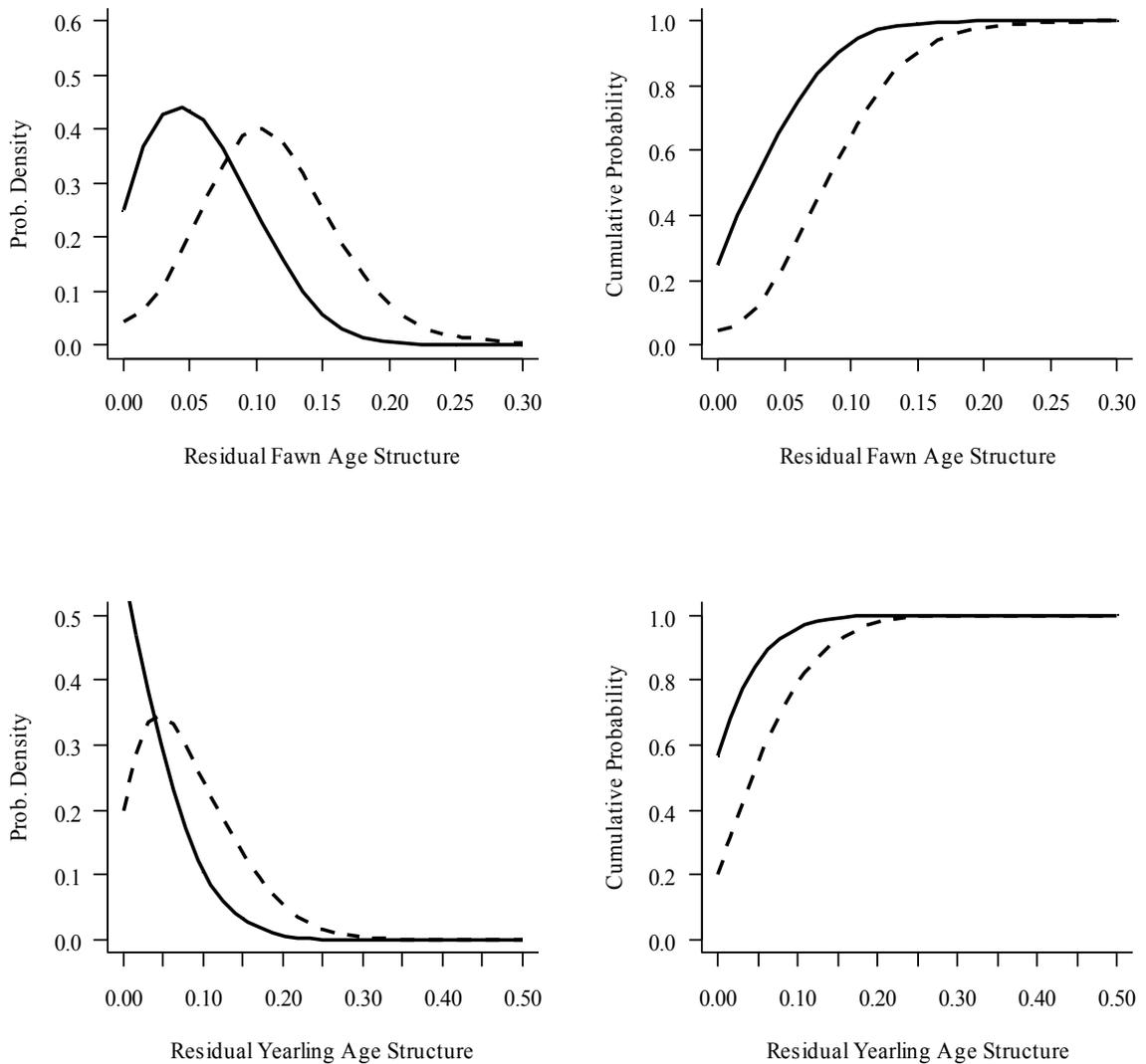


Fig. 10. Predicted probability density and cumulative probability distributions for fawn and yearling male white-tailed deer residual age structure for 2 periods of regulatory restrictions modeled at the regional level (LMAV) (expressed as a proportion of total population). The historical scenario (no antler restriction) is shown as a solid line, and the management scenario (antler restriction) currently in use in Arkansas is shown as a dashed line.

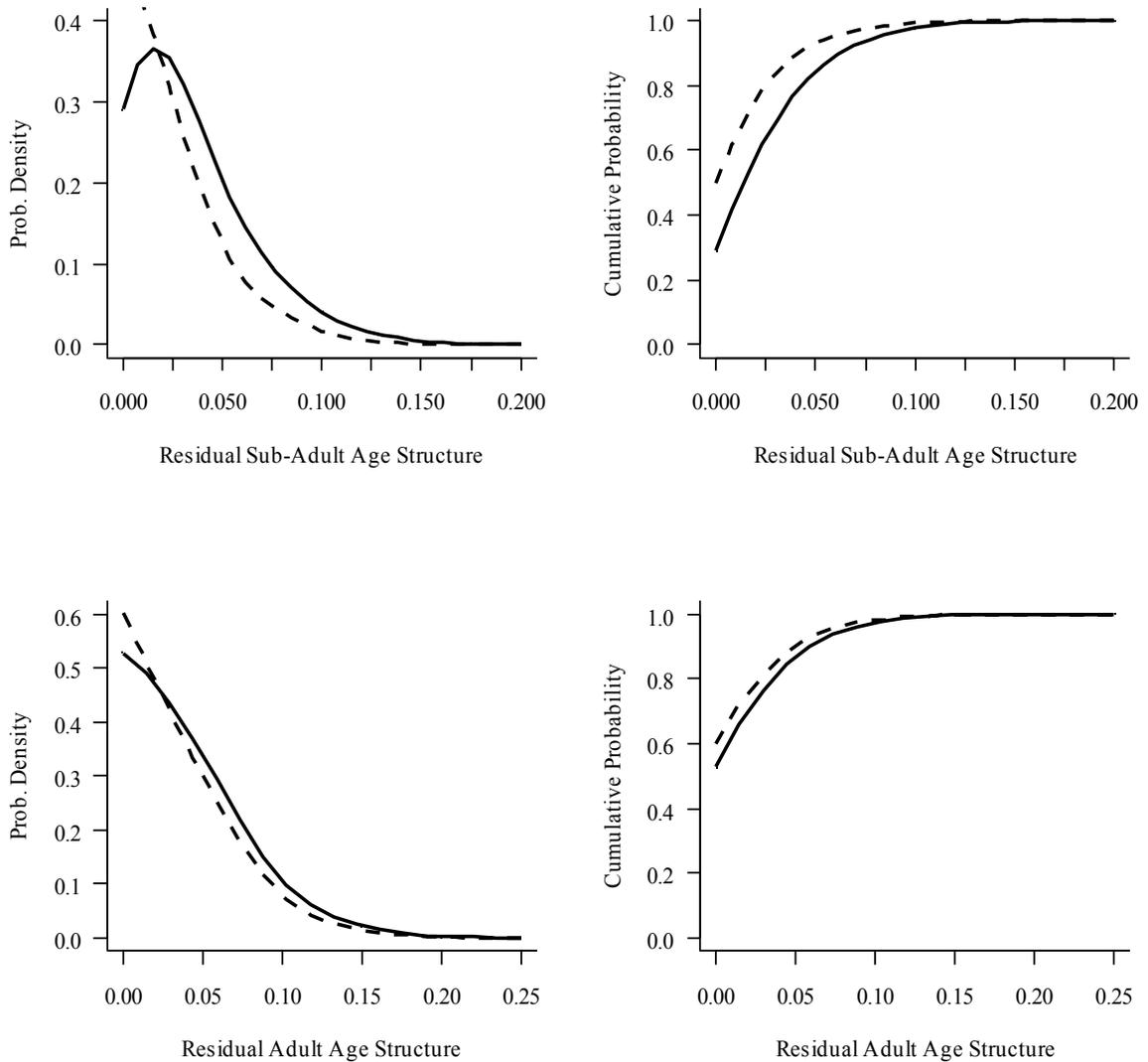


Fig. 11. Predicted probability density and cumulative probability distributions for sub-adult and adult male white-tailed deer residual age structure for 2 periods of regulatory restrictions modeled at the regional level (LMAV) (expressed as a proportion of total population). The historical scenario (no antler restriction) is shown as a solid line, and the management scenario (antler restriction) currently in use in Arkansas is shown as a dashed line.

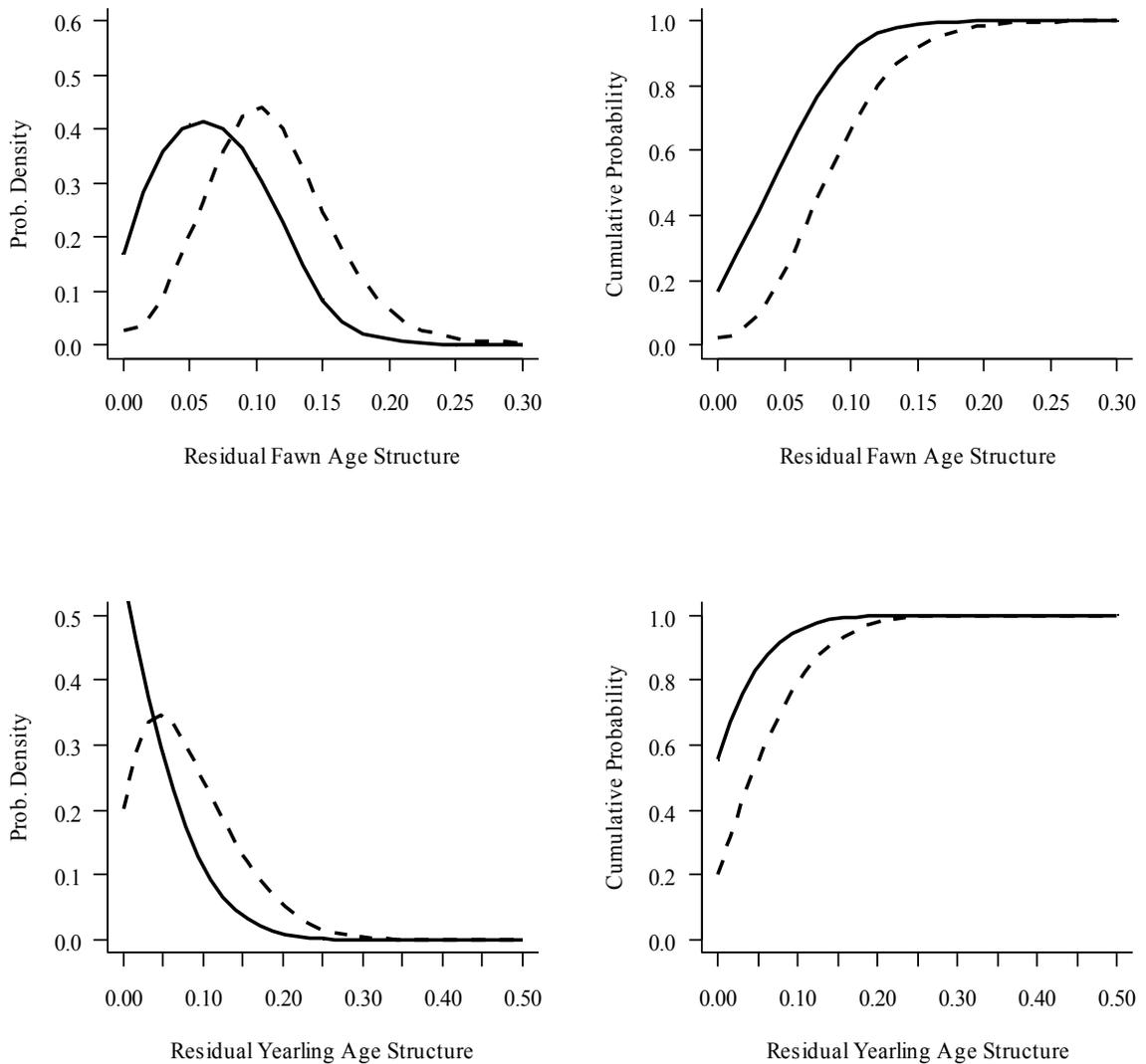


Fig. 12. Predicted probability density and cumulative probability distributions for fawn and yearling male white-tailed deer residual age structure for 2 periods of regulatory restrictions modeled at the state level (expressed as a proportion of total population). The historical scenario (no antler restriction) is shown as a solid line, and the management scenario (antler restriction) currently in use in Arkansas is shown as a dashed line.

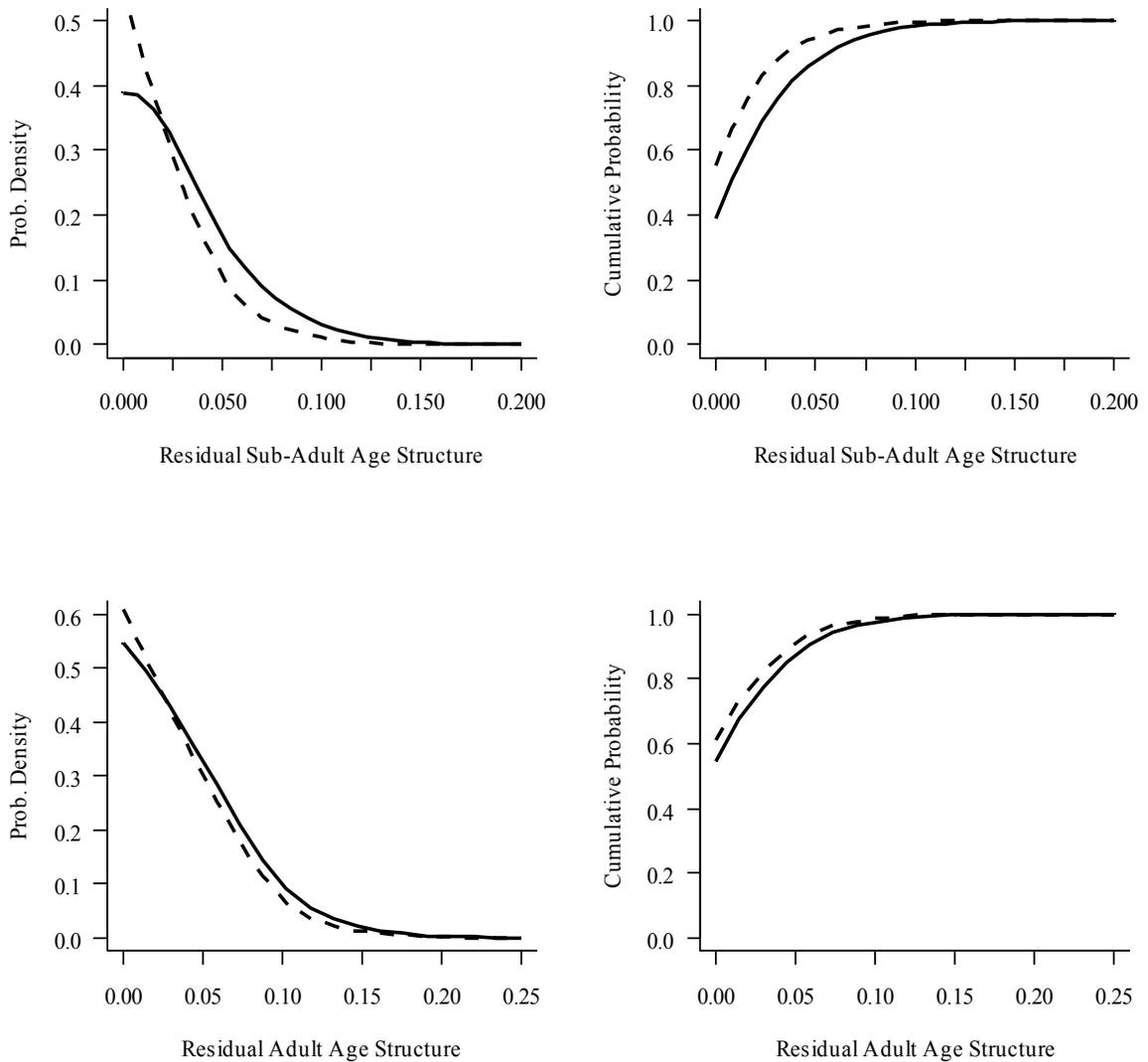


Fig. 13. Predicted probability density and cumulative probability distributions for sub-adult and adult male white-tailed deer residual age structure for 2 periods of regulatory restrictions modeled at the state level (expressed as a proportion of total population). The historical scenario (no antler restriction) is shown as a solid line, and the management scenario (antler restriction) currently in use in Arkansas is shown as a dashed line.

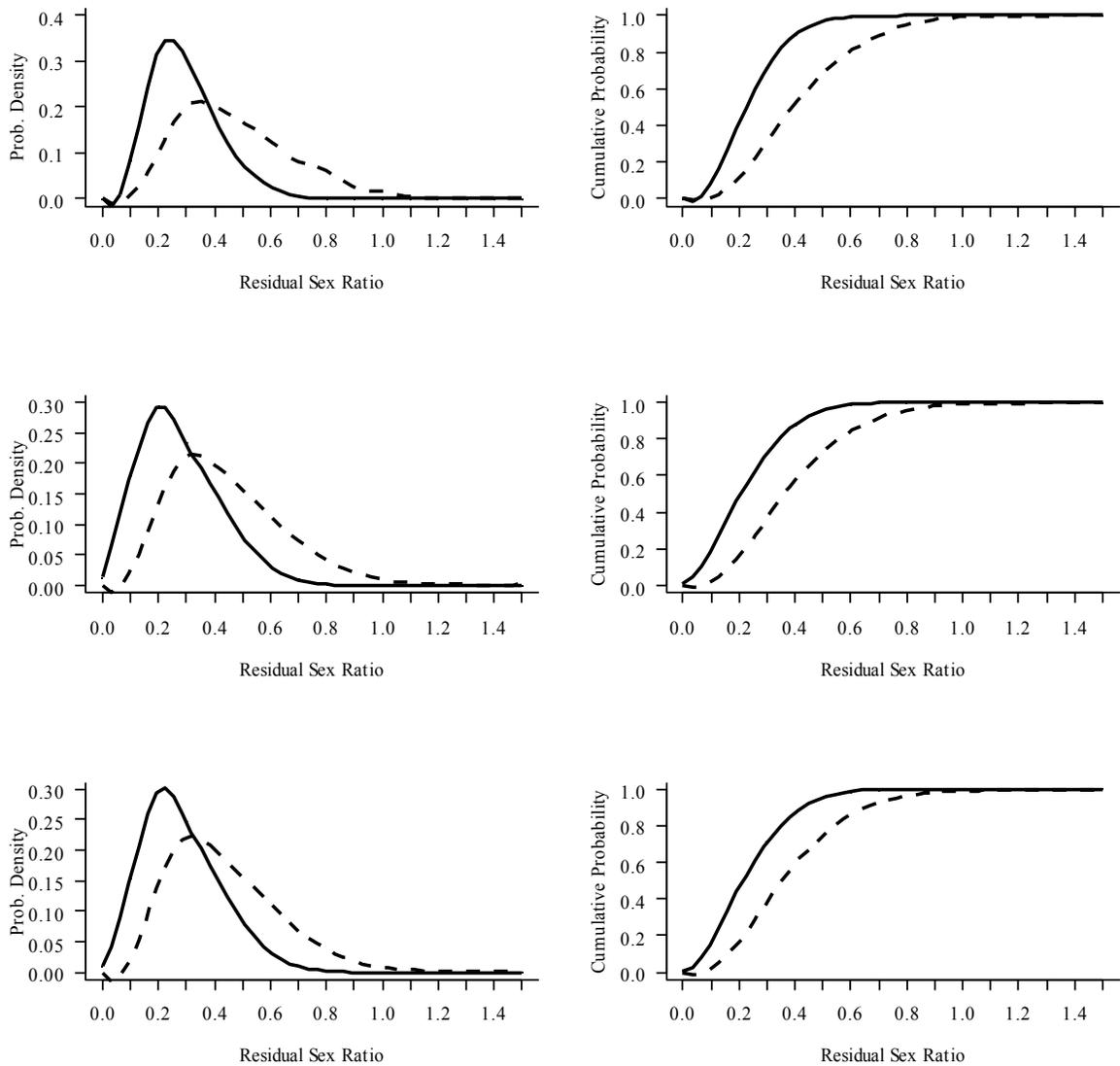


Fig. 14. Predicted probability density and cumulative probability distributions for residual population sex ratio (expressed in No. Males/No. Females) modeled at the county (Arkansas, top), regional (LMAV, middle), and state level (bottom). The historical scenario (no antler restriction) is shown as a solid line, and the management scenario (antler restriction) currently in use in Arkansas is shown as a dashed line.

CHAPTER III. AN ALTERNATIVE APPLICATION OF HARVEST MANAGEMENT PLANNING FOR WHITE-TAILED DEER IN ARKANSAS

ABSTRACT

Predicting structure and the impacts of vital rates and harvest management on white-tailed deer (*Odocoileus virginianus*) populations is a complicated task for managers. Uncertainty associated with population dynamics, accuracy of parameter estimates, and limited knowledge of multiple biological and regulatory factors interact reduced the ability of managers to make informed decisions. Thus, harvest management decisions are being implemented based on *ad hoc* approaches that are untested and based on questionable ecological relationships. In order to account for uncertainty due to limited knowledge, I developed a decision process for managers that explicitly accounts for uncertainty in parameter estimates and provides a graphical interface for evaluating management options. By recasting a stochastic population model in a graphical framework using a Bayesian Belief Network (BBN), I examined predictive ability and expected response of populations to management actions and biological factors for 3 specific hypotheses of the Arkansas Game and Fish Commission. First, I found that knowledge of pre-harvest population structure was important for reducing uncertainty in the residual (post-harvest) population. Second, in order to maximize the residual population of adults (≥ 3.5 years old) reductions in the harvest rate were required, as well as management for the pre-harvest population to exceed 10% of the total population size. Finally, when I examined residual sex ratios, I found that knowledge of the harvest sex ratio was unimportant towards predicting residual sex ratios (reduction of uncertainty

$\leq 10\%$), and that ancillary information collected by archery hunters, if based on a viable sampling protocol, could assist managers in reducing uncertainty when predicting residual population sex ratios ($\geq 70\%$ reduction in uncertainty). I found that combining stochastic population models with graphical modeling has the potential to assist white-tailed deer managers to evaluate and determine appropriate courses of action when planning harvest management strategies and adaptive management actions. My work could benefit deer managers by allowing them to test *a priori* hypotheses and in determining what information is necessary for management purposes.

When planning a harvest management strategy, biologists must adequately consider the purpose of the management to ensure that multiple conflicting goals are not being addressed (Peterson 1999). Development and implementation of deer harvest management strategies are influenced by several factors. Variation in population vital rates, limited availability of population demographic parameters under different management scenarios (McShea et al. 1997), and environmental variation all reduce the ability of biologists to predict population responses. Difficulties associated with identifying which factors influence system dynamics limits plausible designs for deer harvest management programs. As the resulting impacts of management decisions in a biological system are rarely certain, managers need new methods for evaluating hypotheses regarding harvest management approaches in cases where data are limited. For white-tailed deer, the intent of most harvest management practices is to manipulate population structure (age structure, sex ratio) and abundance. Thus, because the ability to specify a system state at a specific place and time is limited (Williams et al. 2002), approaches allowing managers to incorporate known biological information while acknowledging and accounting for uncertainty in those unknown values could benefit management planning and evaluation.

Population models are commonly used to construct and evaluate harvest regulations for game species across the United States (Lubow et al. 2001, White and Lubow 2002). Recent advances in stochastic population modeling (SPM) (Lande et al. 2003, Phillips and White 2003) provide deer managers with an alternative to current informal model designs. Using SPM, researchers can evaluate simultaneous interactions between deterministic and stochastic model components (Lande et al. 2003), temporal

changes in population size and structure (Engen et al. 1998, Lande et al. 2003), and approach management planning using what-if scenarios (Walters and Gross 1972). SPM has been infrequently used by managers, often thought of as a research tool for academia (Phillips and White 2003)

In order to evaluate the impacts of SHC on the response of white-tailed deer populations while accounting for various sources of parameter uncertainty, I developed a stochastic age- and sex-structured population model, which I recast in a probabilistic framework using a BBN implemented in program NETICA 2.17 (Norsys Software Corp). My objective was to develop a modeling process that incorporated available white-tailed deer population parameters with current regulatory restrictions to be used for hypothesis testing, evaluation, and management planning. In order to show the utility of this approach, I provide 2 example applications of the network at the scale of the hunting camp to (1) evaluate which factors (knowledge of population parameters) are needed to assist managers in increasing the frequency of older males in the residual (post-harvest) population, and (2) evaluate knowledge of which factors are needed to assist managers in reaching levels of residual population sex ratio that is considered “optimal”.

METHODS

Modeling Approach

A simplified way of understanding BBNs is to think of a biological system where causality plays a role, but our understanding of the mechanisms linking biological factors is incomplete (Charniak 1991). Thus, the purpose of a probabilistic graphical model is to provide the researcher with a repeatable, quantitatively rigorous means to evaluate population responses given this causality. Evaluation of BBN is based on the basic

mathematical computation of a nodes belief (conditional probability) given the currently observed evidence (data).

To simplify understanding of conditional probability estimation, I provide a simple example of Bayes theorem (Bayes 1763, Lee 2001). For this example, suppose that a state agency suggested a regulatory change that would increase the bag limit of male deer from 2 to 3. After the regulatory change was voted on, 55% (hunters) supported the change, while 45% (non-hunters) did not support the change. Assume that several research studies conducted by the state agency indicated that 90% of hunters and 40% of the non-hunters intended to vote ‘yes’ on changing the bag limit of male deer, while the remainder intended to vote against the change. Having all of this information available, if agency personnel met someone on the street who indicated that they intended to vote ‘yes’, we are interested in determining the probability that this individual is a hunter. Thus, the probabilistic form of this relationship would be expressed as:

$$\begin{aligned}
 P(H | Y) &= \frac{P(Y | H)P(H)}{P(Y | H)P(H) + P(Y | N)P(N)}, \\
 &= \frac{(0.90)(0.55)}{(0.90)(0.55) + (0.40)(0.45)}, \\
 &= 0.733,
 \end{aligned}$$

where $P(H)$ is the probability an individual is a hunter, $P(N)$ is the probability an individual is not a hunter, $P(Y | H)$ is the probability an individual votes yes for the change in regulations, given they are a hunter, $P(Y | N)$ is the probability an individual votes yes for the changes in regulations given they are a non-hunter, and $P(H | Y) =$

0.733 is the probability of an individual being a hunter conditional on the individual voting yes.

Following along from the previous example, the CPT for the node Hunter would be represented by Table 1. The CPT for the conditional relationship between the node representing hunters and the node which represents favoring or opposing changing the bag limits (Voters) is shown in Table 2. In a BBN, the following example would be constructed using these underlying estimates and the structure, shown in the models initialized condition in graphical (node) form (Fig. 1). Whereas we know that an individual approached by agency personnel voted ‘yes’, we can then incorporate this information into the model structure (model updating) and update our belief (posterior estimate) that the individual is a hunter (Fig. 2). Note that the updated belief (Fig. 2) that the individual was a hunter agrees with the previously estimated belief (formula at top of page) that an individual was a hunter given that they voted “yes” ($P(H | Y)$) was 73.3% (0.733).

In contrast to most wildlife modeling approaches, BBNs use probabilistic expressions describing the relationships between variables (Borsuk et al. 2004). Belief vector structure is based on user-defined bin-widths which then create belief histograms (Fig. 3). Bin widths, or the range of the axis covered by each bar within the graphical structure, generally refer to a specified range that a vital rate can take (Lee and Rieman 1997). Because the “true” state of a variable is rarely known, uncertainty is indicated by assigning belief to each range of values within a node (Lee and Rieman 1997). As belief can never be >1 (e.g. 100%), the allocation of belief within each node given the defined bin-width sizes is used to show the certainty (or uncertainty) associated with the state of

each biological variable within the system. Discrete categories (discrete response states, e.g. yes/no) can be explicitly defined for each plausible state within the graphical model, while the bin width size for continuous variables can be defined by the user.

In order to provide a realistic example of this approach, I recast the stochastic population model (described in Chapter 2) into a probabilistic graphical model using program NETICA. The casual linkages (arrows) define the conditional probabilistic relationships which underlie the graphical structure. For each node, there exists a conditional probability table (CPT; see above example) that probabilistically describes the relationships between node values. Input nodes were defined as those nodes specifying a prior (unconditional) probability, or the likelihood that a parameter is in a specific state (Example shown in Table 1). Conditional probabilities for each non-root node represent the likelihood that the parameter is in a specific state, conditional on the state of the input nodes affecting it (Marcot et al. 2001, Lee 2002). In the models initialized state (Fig. 1 in example), the histograms for each node represent the marginal probabilities (belief vectors) for that node (Fig. 3). To graphically represent parameter uncertainty, the probabilistic representations (belief vectors) for each node in my approach that represented a continuous variable was divided into 5 to 10 discrete levels (Lee and Rieman 1997, Marcot et al. 2001). Deterministic nodes were discretely specified.

Conditional Probability Estimation

In order to estimate conditional probabilities used in my probabilistic model, I used an approach patterned after Lee and Rieman (1997), Peterson and Evans (2003), and Steventon et al. (2003). Using an external stochastic population model, I output a file of

model results, which I used to parameterize the nodes within the network. Because parameter uncertainty works in concert with variability in biological systems, I used the combination of a large number of model runs to estimate probabilities of various population responses while accounting for uncertainty in the system. I conducted 500,000 simulations using random combinations of input parameter estimates that were representative of white-tailed deer in Arkansas and across the U.S. (see Chapter 2 for parameter descriptions). After simulating white-tailed deer population dynamics for a 20-year period, the resulting output at the 20th year was used to parameterize the CPT within the graphical structure using a case file format. Model created case files are a database of findings including values for input parameters, model created intermediate variables, and modeled output variables of interest (Steventon et al. 2003, Peterson and Evans 2003). The case file, when loaded into the network, specifies the joint distribution between connected nodes.

HYPOTHESIS TESTING AND EVALUATION

In this section, I provide 3 examples that test and evaluate hypotheses related to Arkansas Game and Fish Commission (AGFC) white-tailed deer management strategies. First, I evaluated the impact of changing pre-harvest population structure, harvest rates, regulatory restrictions, and the resulting effects on residual population age structure for sub-adult males (2.5 years old). I then evaluated what factors managers would need to maximize the residual male adult population. Finally, I evaluated the impacts of several different data sources on the prediction of residual (post-harvest) population sex ratio. Throughout this discussion, node names will be highlighted using an italics script (e.g. *Residual Male Subadult*).

Hypothesis 1: Evaluating Residual Male Sub-Adult Population Structure

I evaluated the population response of the sub-adult age class (*Residual Male Subadult*), in initialized form (after the case file had been incorporated, but no updating had been conducted, Fig. 4). In the sub-adult model initialized form, with no knowledge incorporated into the model, a majority of the predicted belief for the residual population of sub-adults (*Residual Male Subadult*) was expected to fall between 0 and 2.5% of the total population (51.8%), with 82.5% (51.8 + 30.7) of the belief concentrated at $\leq 5\%$ of the total residual population (Fig. 4). Assuming that the AGFC was evaluating harvest regulations before the opening of hunting season, and that the regulatory restriction was in use, by changing the value for *Regulations* to In Effect, there was a slight shift in the belief structure for *Residual Male Subadult*, where the belief that the population will fall below 2.5% of the total population declined 2.7% to 49.1%. Also, belief that the population will fall between 2.5% and 5% of the total population increased 1.2% to 31.9% (Fig. 5). Should information become available (using various biological surveys) showing the pre-harvest male sub-adult population (*Male Sub Adult*) was between 5% and 10% of the total population, updating pre-harvest male sub-adult information changes belief in the response of the *Residual Male Subadult* population. In this example, belief that the sub-adult population would be between 0% and 2.5% of the total population was 27%, between 2.5% and 5% was 41%, and between 5% and 7.5% was 24% (Fig. 6).

To evaluate the impacts of knowledge of the age structure of the harvest (Figs. 7 and 8), I manipulated the harvest data node (*Male Sub Adult Harvest*) to the outer boundaries of the range of harvest data collected by the AGFC on an annual basis (while making no other changes to the model). Setting the harvest data to between 27% and

32% of the total male harvest, there was a slight decrease (2%) that the *Residual Male Subadult* population will fall between 0% and 2.5% of the total population (Fig. 7).

There was a 4.2% increase that the population will fall between 2.5% and 5% of the total population (Fig. 7). In the opposite direction (Fig. 8), by constraining harvest of sub-adult males to be between 40% and 44% of the total male harvest, belief that the *Residual Male Subadult* population will be between 0% and 2.5% of the total population increased to 56.1% (a 4.3% increase). There was also an 8.2% increase in belief that the *Residual Male Subadult* population will fall between 2.5% and 5% of the total population (now 38.9%).

Using the initialized conditions model (Fig. 4), applications where new information (knowledge) was incorporated into the model structure can provide “most likely” states for input nodes. As an example, in Figure 9, I updated belief that *Residual Male Subadult* population was known to be between 0% and 2.5% of the total residual population. There was a 26.5% increase in belief that the pre-harvest population (*Male Sub Adult*) fell between 0% and 5% of the total population (56.3% to 72.8%) as well as a 2.6% decline in the belief that the regulatory restrictions (*Regulations*) were In Effect (50% to 47.4%). Also note that belief in the harvest rate (*Rate (Sub Adult)*) shifted downward to higher harvest rates (Fig. 9). On the opposite end, assume that the manager wants to maximize the residual male sub-adult population. By setting *Residual Male Subadult* to be $\geq 15\%$ of the total population, there was a 27.5% increase in the belief that *Rate (Sub Adult)* was between 100% and 125% of harvest data. There was also a 5% change in belief that the *Regulations* were In Effect (Fig. 10).

Assuming that we have complete knowledge at the hunting camp scale of all population parameters and harvest information, this information can be included into the graphical structure to show the most likely response of the sub-adult male population (Fig. 11). Note that even with complete specification of all nodes influencing the *Residual Male Subadult* node, there was still some uncertainty associated with the population response as belief is spread across 3 population response categories (0-2.5%- 79.6; 2.5%-5%- 17.0; and 5%-7.5%- 2.82) (Fig. 11).

Changing the regulations to be In Effect indicated that the residual population age structure for sub-adult males would increase. Incorporating knowledge of the pre-harvest population age structure shifted the residual population age structure predictions to encompass a smaller range of belief (e.g. reduced uncertainty). Knowledge of the harvest data had little impact on residual population age structure.

Hypothesis II. Maximizing Adult Male Residual Population

In this example, I evaluated the population response of the adult age class (Residual Male Adult) to various perturbations. The model subset in initialized form (after the case file had been incorporated, but no updating had been conducted) indicated that the residual population of adults was not concentrated in one specific level (Fig. 12). Thus, there was uncertainty in the belief of a specific population response. As shown in Figures 13 and 14, knowledge of whether the regulatory restriction (*Regulations*) is In Effect or Not In Effect had little influence on reducing uncertainty in the residual population response (*Residual Male Adult*) as the belief vector was not concentrated in any one value or small range of values, but spread across the entire node. If the management interest was to maximize the residual male adult population, by updating

Residual Male Adult to be ≥ 0.15 (residual male adult population was greater than 15% of the total population) belief vectors for pre-harvest population (*Male Adult (Pre-Harvest)*) and harvest rate (*Rate (Adult)*) both shift. *Male Adult (Pre-Harvest)* shifted to higher levels of pre-harvest population (e.g. 68.5% of belief fell where the pre-harvest population must be $\geq 10\%$), while the *Rate (Adult)* values shifted to a lower level of the rate function (e.g. 90.8% of belief fell where the rate function must be $\leq 175\%$) (Fig. 15).

In order to maximize residual male adult populations, my model predictions indicated that managers should attempt to manipulate the population to levels where the pre-harvest male adult population is $>15\%$ of the total population. My model also suggested that reductions in harvest rates were required in order to maximize the adult male residual population.

Hypothesis III. Evaluating Residual Population Sex Ratio

In order to evaluate those factors that influence white-tailed deer residual (post-harvest) sex ratio, I evaluated the influence of having pre-harvest sex ratio information available or management through sex ratio data collection by archery hunters before the opening of modern gun seasons. I define sex ratio as the number of males/number of females (e.g. 1 male/2 females = .5). I evaluated the population response of the adult age class (*Resid Sex Ratio*) after the case file had been incorporated, but no updating had been conducted. In the sex ratio models initialized form, (Fig. 16) the predicted belief for the residual population sex ratio was not concentrated in one specific level (indicating uncertainty in belief of a specific population response).

Knowledge of whether the regulatory restriction (*Regulations*) was In Effect or Not In Effect had little influence on reducing uncertainty in the residual population

response (*Resid Sex Ratio*) as the belief vector was not concentrated in any one value or small range of values, but spread across the entire node (Figs. 17 and 18). However, when regulatory restrictions were Not In Effect, there was a higher propensity for the harvest sex ratio to be ≥ 1 (males/females; belief = 31% versus 18.9% when *Regulations* were In Effect) indicating that males were being harvested in excess of females, which is common under traditional deer management practices.

Across the range of harvest sex ratio (*Harvest Data Sex Ratio*), there was little reduction in uncertainty when predicting the residual population sex ratio (*Resid Sex Ratio*) (Figs. 19 and 20) as the belief vectors were widely spread across possible responses. Incorporating knowledge regarding pre-harvest sex ratio (*PreHarvest Sex Ratio*), of between 0.3 and 0.4 (approximately 1 male to 3 females), there was a reduction in the range of plausible responses for *Resid Sex Ratio* (Fig. 21).

Both examples above agree with results found in Chapter II that knowledge of harvest sex ratio was not important for predicting residual population sex ratio, but that pre-harvest sex ratio information would reduce uncertainty when predicting residual sex ratio. If a management objective was to reach a residual population sex ratio of 1 male to 2 females, with no other information included in the model, then the BBN suggested that *Preharvest Sex Ratio* structure would need to fall between 0.3 and 0.7 (Fig. 22).

My model predictions showed that to accurately predict residual population sex ratio, managers need information on the pre-harvest sex ratio. Harvest regulations currently used increased the residual sex ratio to levels of 1 male to 2 females, but there was still uncertainty associated with those estimates. My model suggested that harvest sex ratio influenced residual sex ratio predictions.

DISCUSSION

As wildlife agencies are being required to evaluate the plausible impacts of harvest management decisions, techniques that allow managers to evaluate biological mechanisms for these actions while accounting for uncertainty due to limited data availability are needed. When planning management practices for wildlife, use of population models has become common for most species (White and Lubow 2002). However, sufficient data to evaluate model structure and test underlying assumptions regarding the mechanistic relationships between population parameters are often unavailable. Uncertainty associated with model parameters and model form limits managers in their ability to predict future states (Lee and Rieman 1997, Marcot et al. 2001). By combining a stochastic population model with a BBN, deer managers can combine information from multiple research studies, illustrate suspected causal relationships between population parameters, and provide a graphical representation of uncertainty associated with population and response parameters of interest.

Graphical analysis provides the researcher with an approach that contrasts to historical modeling approaches. First, graphical analysis allows the managers to create figures showing plausible ranges of population response values across a specific set of input variables or model scenarios. This contrasts to commonly used modeling approaches where summary statistics are output (either as figures or tables) which typically provide a less complete depiction of the response distribution (Bender and Roloff 1996, Alipzar-Jara et al. 2001, Phillips and White 2003). Also, the graphical approach allows managers to incorporate additional empirical information by simply redefining the belief for each node, limiting the need for continuous model re-evaluation,

which would be necessary as additional information becomes available. Because population parameters were constructed to encompass a viable range of vital rates, population responses can be examined across a range of parameter values.

Although beneficial, use of BBNs for management planning and evaluation has several deficiencies. Current model structure does not allow for feedback loops or time-dependent modeling (Marcot et al. 2001, Borsuk et al. 2004, although see Haas 1992), which could limit application for researchers evaluating temporal effects due to time lags in population responses. BBN modeling suffers the same shortfalls as other modeling approaches as models are nothing more than caricatures of reality used to provide a representation of a system at a particular place and time (Borsuk et al. 2004). Thus these models are only as good as the assumptions that are defined up front.

I evaluated the BBN approach in a series of applications examining specific questions posed by Arkansas Game and Fish Commission (AGFC) staff. Efficient management of white-tailed deer populations requires that applications which combine research and management goals with the values and preferences of those individuals influenced by the management decision all be incorporated into a single decision making process (Peterson 1999, Peterson and Evans 2003). By illustrating these questions in a probabilistic graphical framework, deer managers in Arkansas have the ability to examine the potential impacts of harvest management strategies, evaluate which parameters most influence population responses of interest, and identify variables which require future research and monitoring (Peterson 1999).

Efficient management and monitoring of population responses to management actions requires that managers develop and apply methods that combine information from

multiple disciplines into an integrated framework (Lee and Rieman 1997, Peterson 1999, Marcot et al. 2001, Peterson and Evan 2003, Borsuk et al. 2004). Although limited applications of graphical models have been applied in ecological sciences (Peterson and Evans 2003), I found that due to the simplicity and transparency of this approach, probabilistic graphical models have the potential for assisting with difficult management decisions for wildlife managers across the United States.

CONCLUSION

The modeling approach demonstrated here allows white-tailed deer managers in Arkansas to evaluate impacts of harvest regulations on white-tailed deer population age structure and sex ratio. Several conclusions were reached based on my research. First, information on the age structure of the population before harvest was needed to reduce uncertainty in residual population age structure predictions for sub-adult and adult age male age classes. Second, in most deer management applications harvest data has been the primary data source used for population management and monitoring. Based on my results, the use of harvest data was insufficient for reliably predicting residual population age structure. Third, if the management objective was to maximize the residual male adult population, my research suggested that pre-harvest population structure of adult males should be $\geq 10\%$ of the total population, and that harvest rates should be reduced. Fourth, while information on harvest sex ratios was of limited value for predicting residual population sex ratio, my results suggested that these predictions could be enhanced if pre-harvest sex ratio information was incorporated in the model. I suggest that management strategies should focus on estimating population structure (age and sex) before harvest, and estimating harvest rates. Future research should address the potential

for alternative model forms and the relationships between harvest, population status, and harvest regulations.

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TABLES

Table 1. Conditional probability table (CPT) for the example node where voters either favored or opposed the change in bag limits. Voters were classified as either favoring (hunters) or opposing (non-hunters) the change (values expressed in %).

	<u>Yes (Hunters)</u>	<u>No (Non-Hunters)</u>
Voters	55	45

Table 2. Conditional probability table (CPT) for the example node regarding whether a hunter or non-hunter favors or opposes the increased bag limits for male white-tailed deer (values expressed in %).

	<u>Favor</u>	<u>Oppose</u>
Hunter	90	10
Non-Hunter	40	60

FIGURES

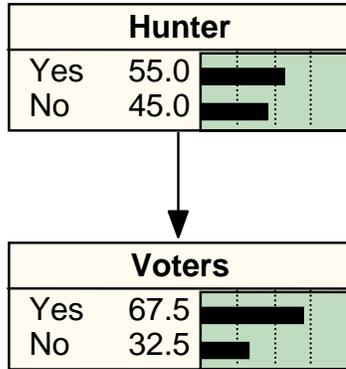


Fig. 1. Initialized model conditions for the example described in text shown in a probabilistic graphical model implemented in Program NETICA.

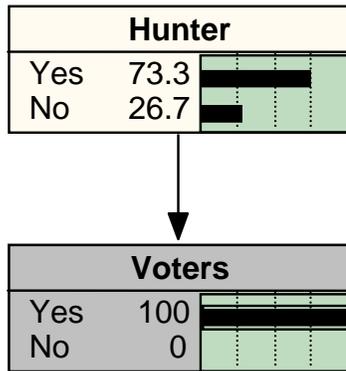


Fig. 2. Updated model conditions for the example described in the text to determine whether an individual was a hunter given that the individual voted Yes (gray box) to the increase in bag limits.

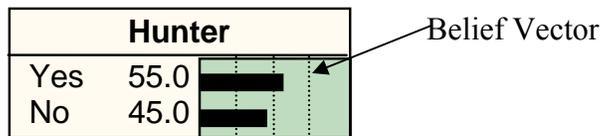


Fig. 3. Belief vector structure for the example described in the text showing the user-defined bin-widths that created the belief histogram.

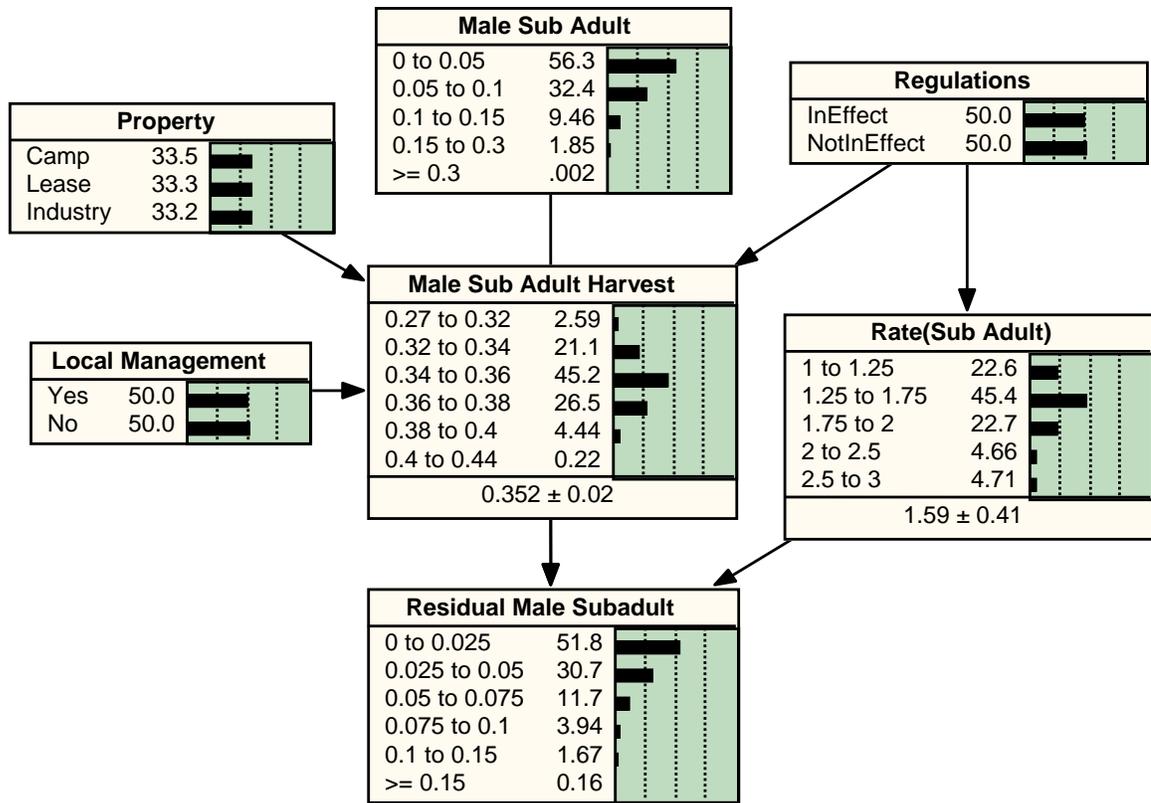


Fig. 4. This figure depicts a subset of the probabilistic network for residual male subadults in the initialized state based on output from the population model at the local scale in Arkansas. Values associated with the histogram bars represent the probability that the parameter is in a particular state.

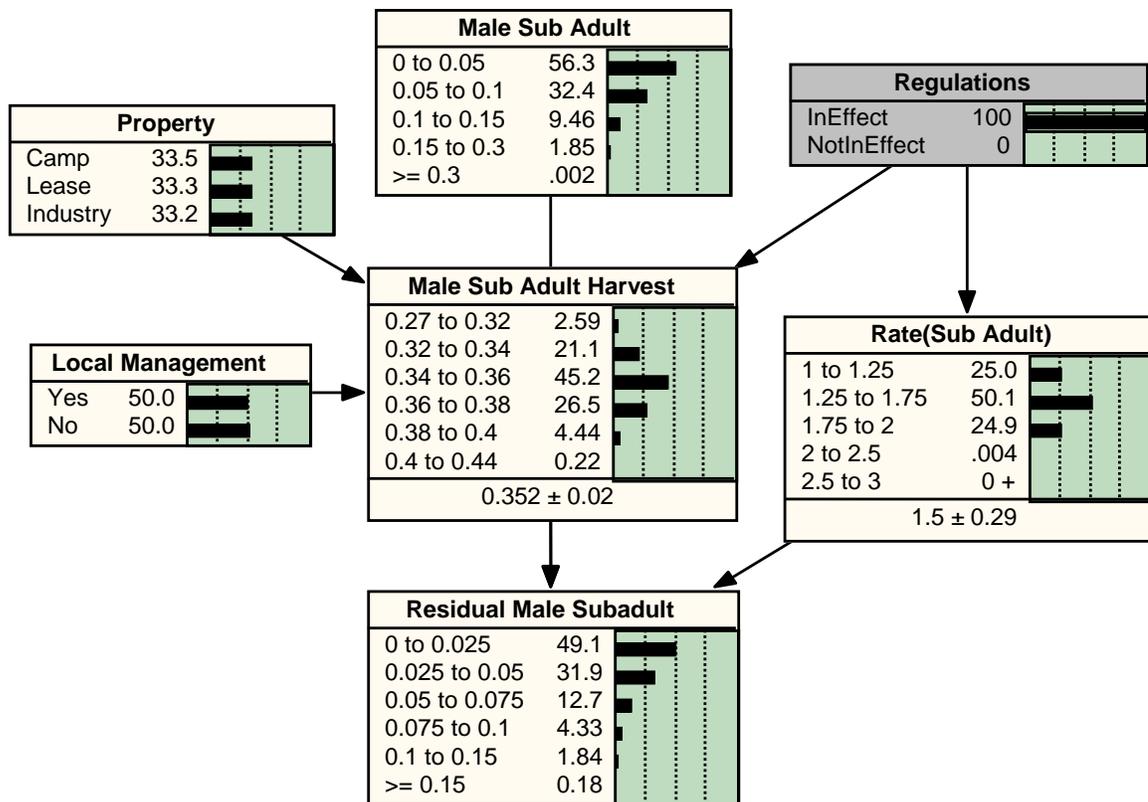


Fig. 5. Probabilistic network in an updated form where information on white-tailed deer harvest regulations has been incorporated into the model (e.g. Regulations=In Effect; gray box) to evaluate the possible responses of the residual sub-adult male population to the regulation at the local scale in Arkansas. Values associated with the histogram bars represent the probability that the parameter is in a particular state.

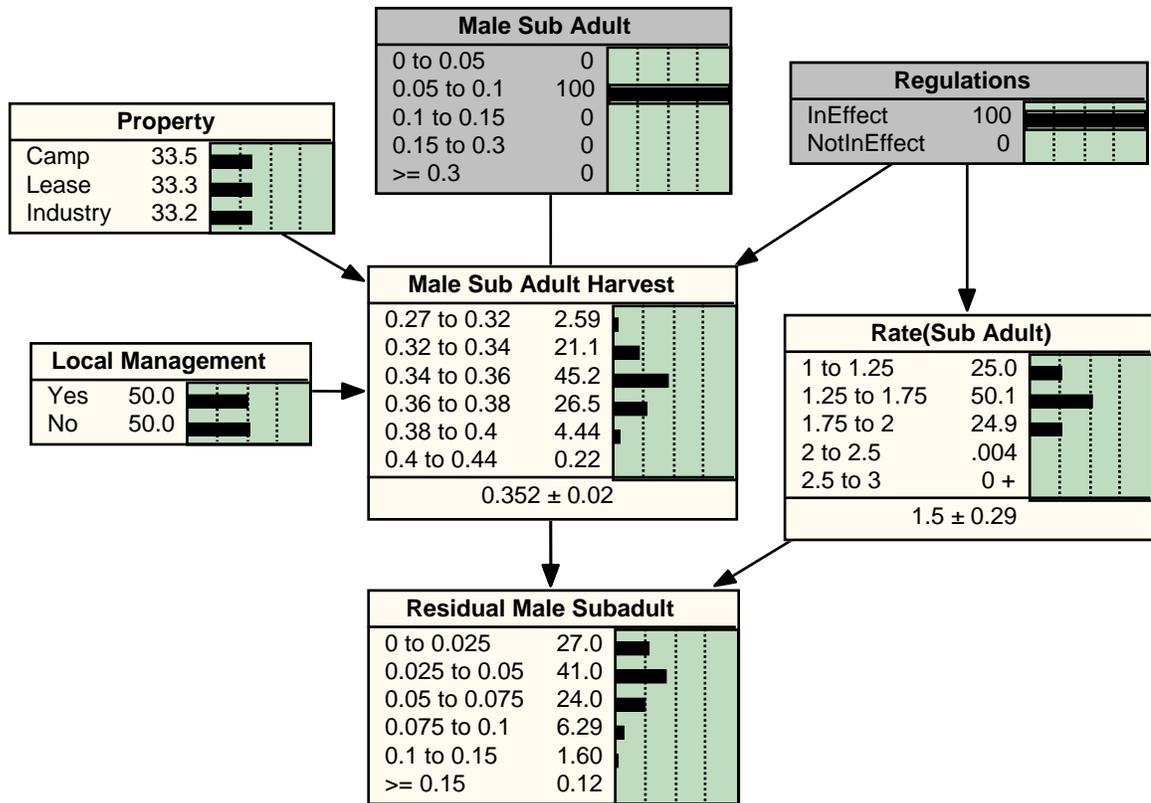


Fig. 6. Probabilistic network in an updated form where information on white-tailed deer harvest regulations and pre-harvest population age structure (gray boxes) has been incorporated into the model to evaluate the possible responses of the residual sub-adult male population to the regulation and knowledge of the pre-harvest population age structure at the local scale in Arkansas. Values associated with the histogram bars represent the probability that the parameter is in a particular state.

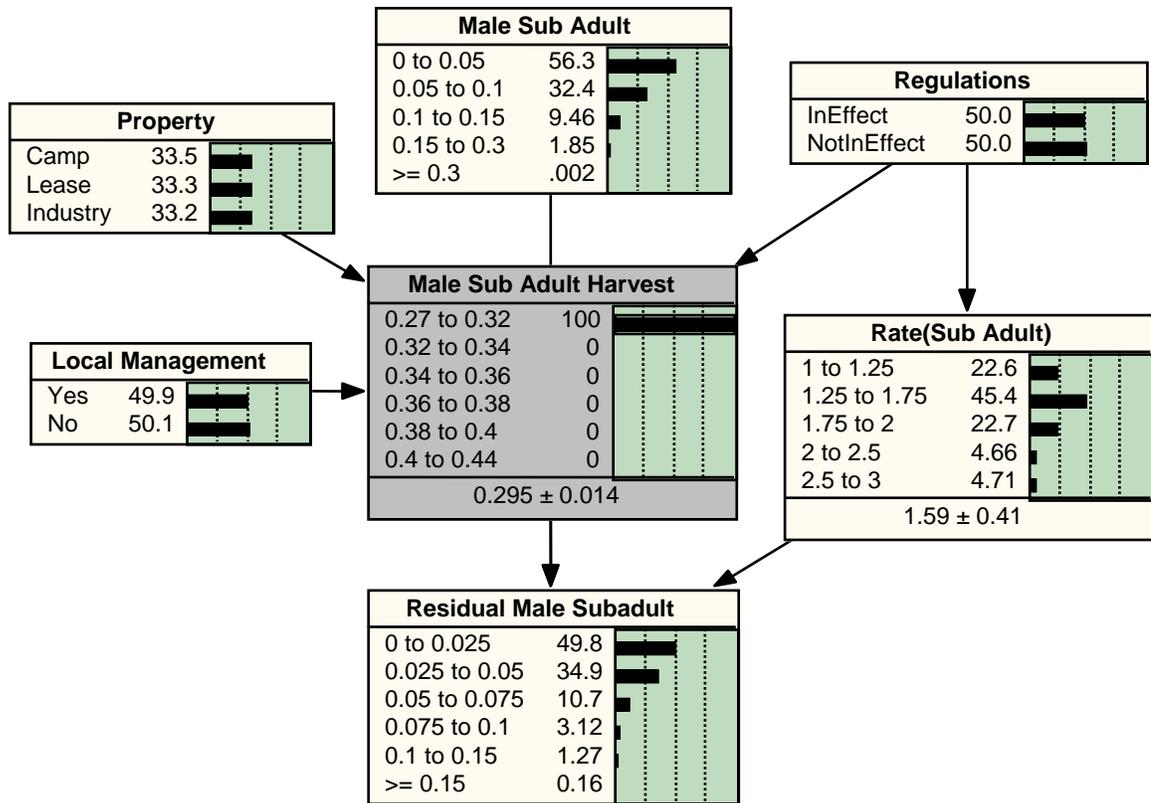


Fig. 7. Probabilistic network in an updated form where information on white-tailed deer harvest (proportion of male sub-adults in male harvest; gray box) has been incorporated into the model to evaluate the possible responses of the residual sub-adult male population to the biological data collected at check stations at the local scale in Arkansas. Values associated with the histogram bars represent the probability that the parameter is in a particular state.

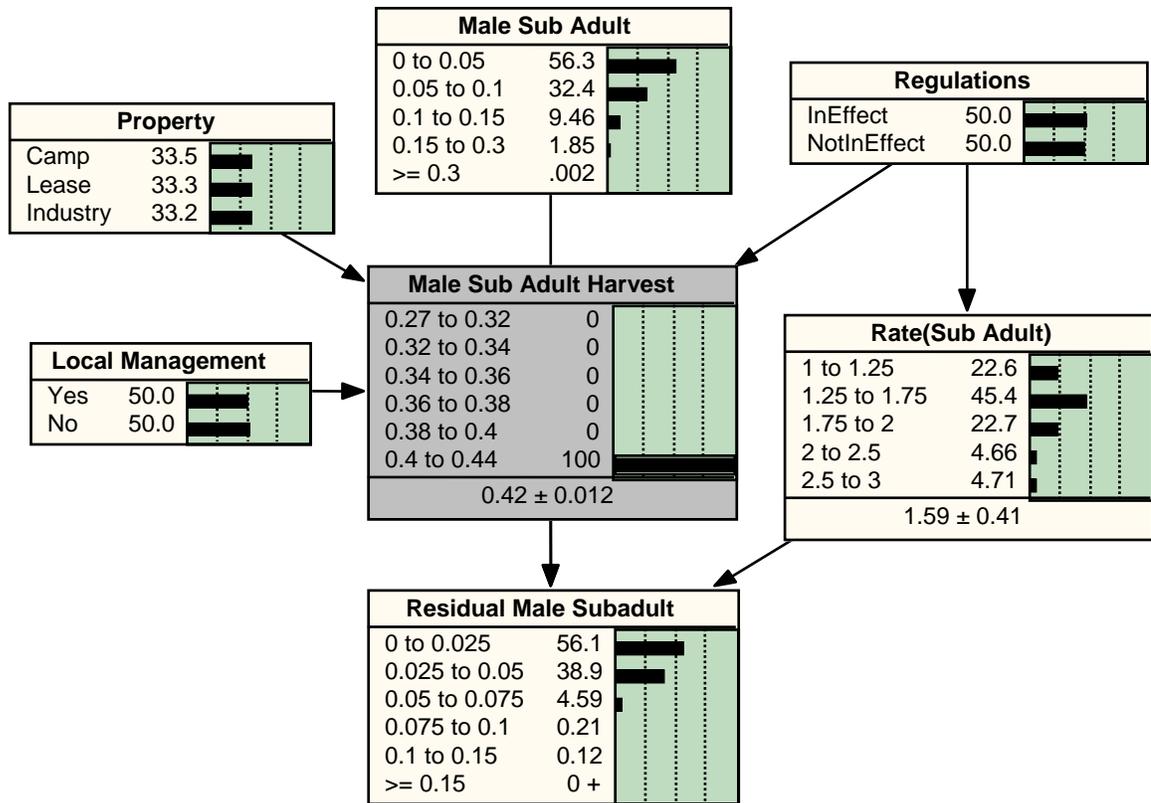


Fig. 8. Probabilistic network in an updated form where information on white-tailed deer harvest (proportion of male sub-adults in male harvest; gray box) has been incorporated into the model to evaluate the possible responses of the residual sub-adult male population to the biological data collected at check stations at the local scale. Values associated with the histogram bars represent the probability that the parameter is in a particular state.

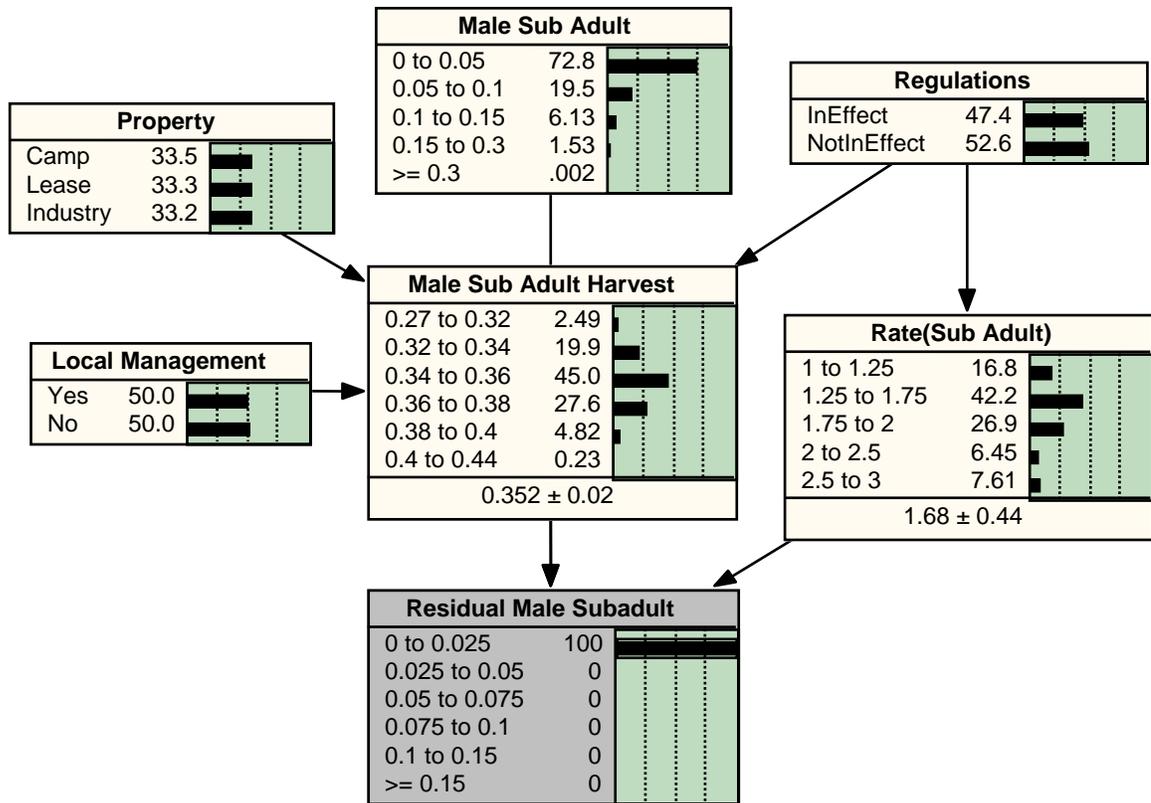


Fig. 9. Probabilistic network in an updated form where Bayesian updating was used in order to determine the ‘most likely’ states of model nodes given that the residual sub-adult male age structure of the population is known (gray box) at the local scale in Arkansas. Values associated with the histogram bars represent the probability that the parameter is in a particular state.

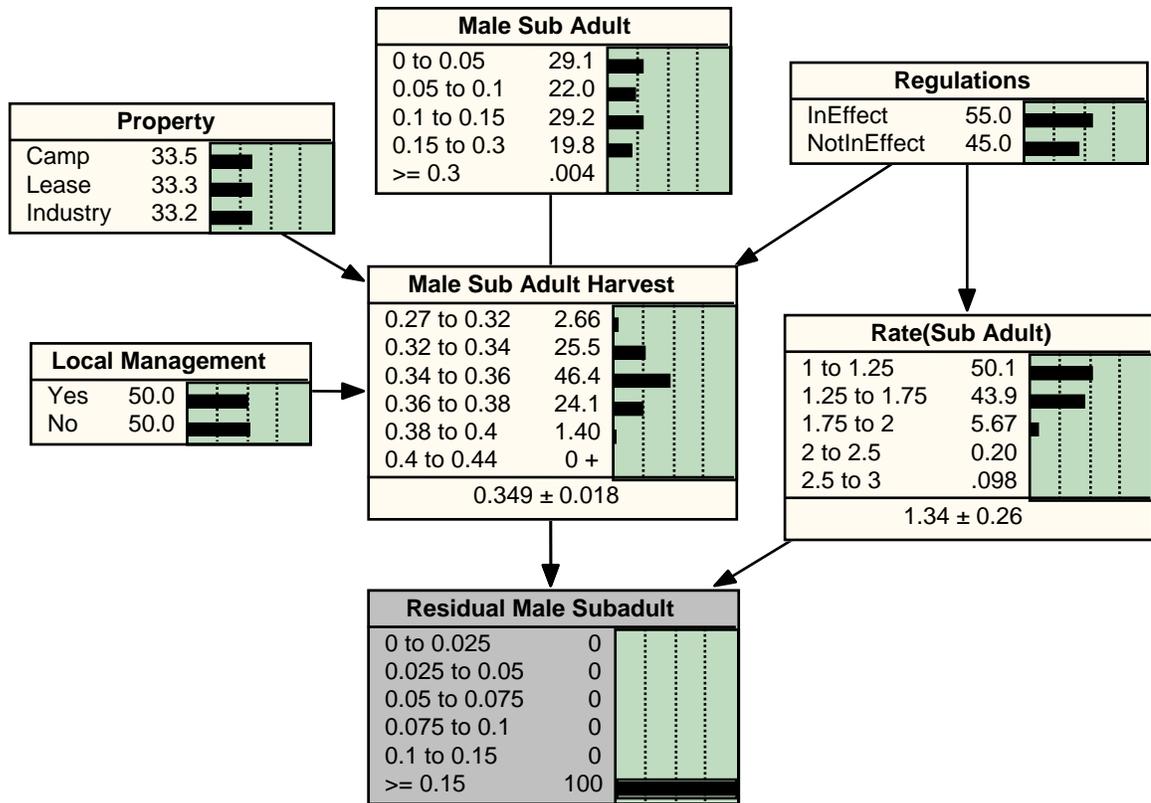


Fig. 10. Probabilistic network in an updated form where Bayesian updating was used in order to determine the ‘most likely’ states of model nodes given that the residual sub-adult male age structure of the population is known (gray box) at the local scale in Arkansas. Values associated with the histogram bars represent the probability that the parameter is in a particular state.

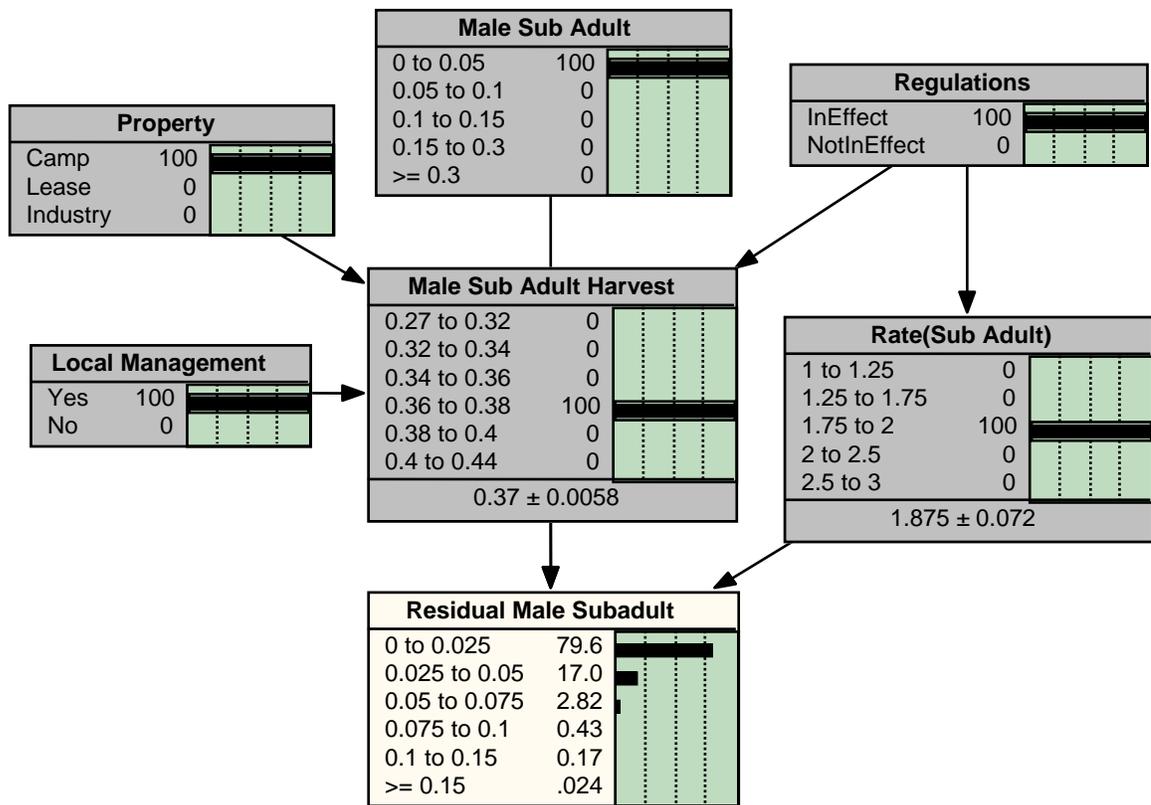


Fig. 11. Probabilistic network in an updated form where each node within the network was completely specified (gray boxes) in order to determine the ‘most likely’ state of the residual male sub-adult population at the local scale in Arkansas. Values associated with the histogram bars represent the probability that the parameter is in a particular state.

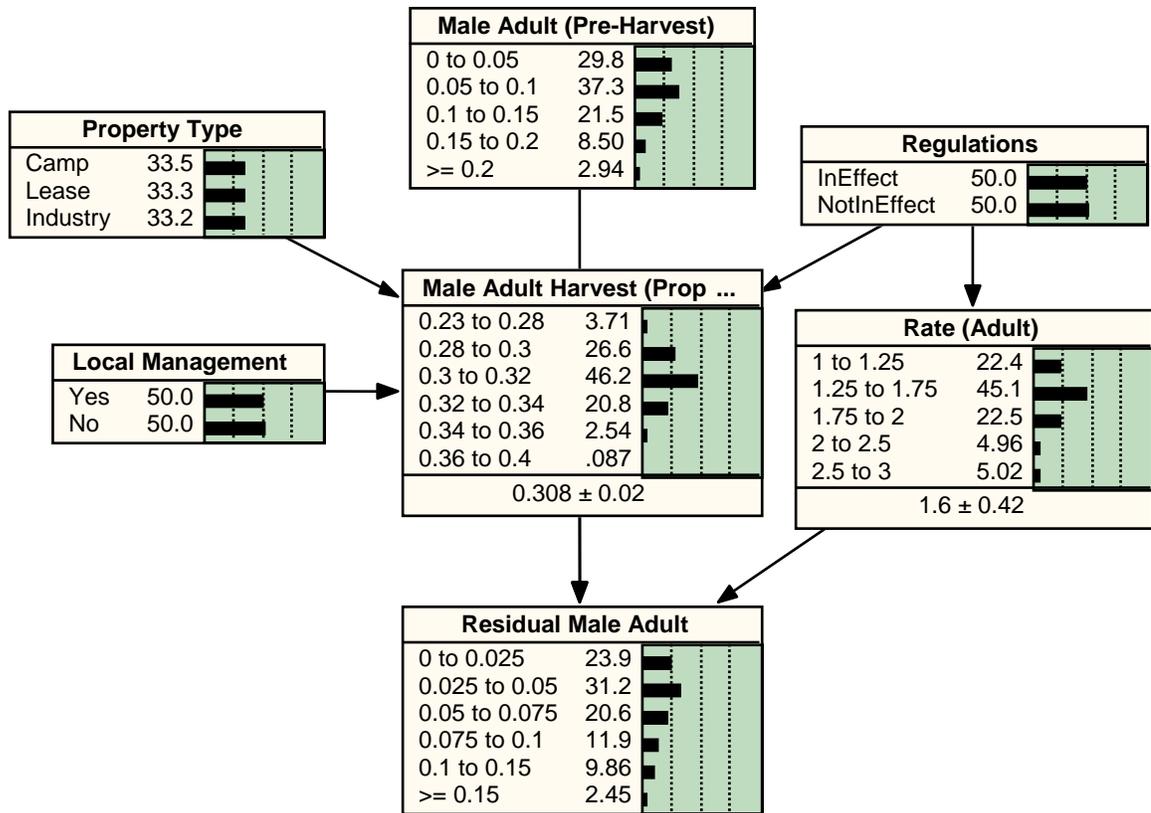


Fig. 12. This figure depicts a subset of probabilistic network in its initialized state based on output from the population model for evaluating the population response of residual male adults at the local scale in Arkansas. Values associated with the histogram bars represent the probability that the parameter is in a particular state.

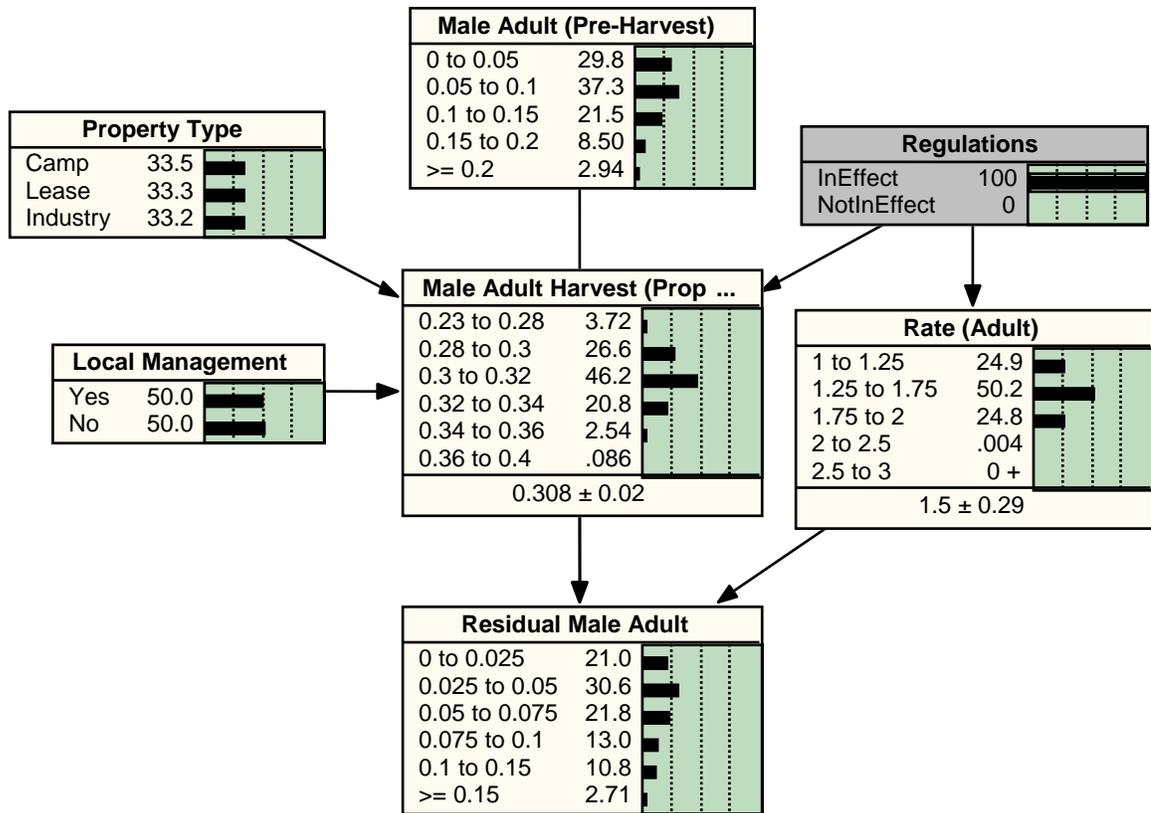


Fig. 13. Probabilistic network in an updated form where information on white-tailed deer harvest regulations has been incorporated into the model (e.g. Regulations=In Effect; gray box) to evaluate the possible responses of the residual adult male population to the regulation at the local scale in Arkansas. Values associated with the histogram bars represent the probability that the parameter is in a particular state.

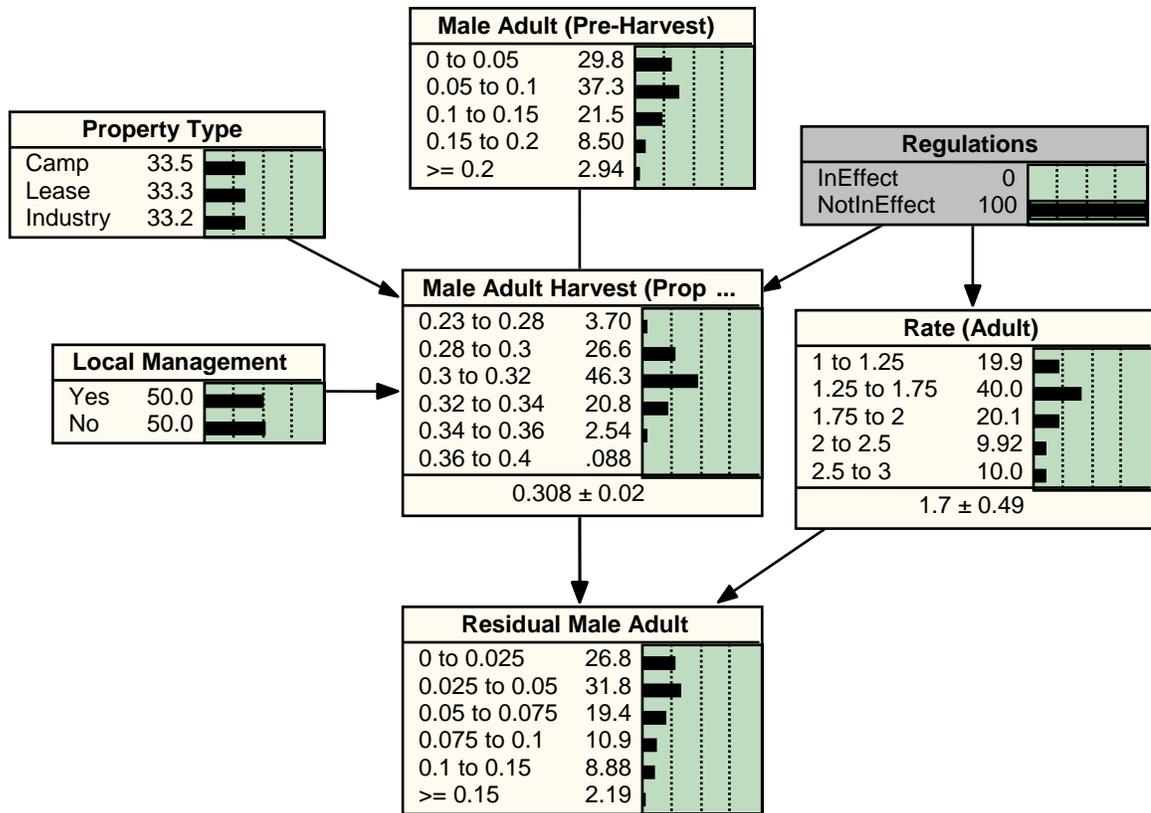


Fig. 14. Probabilistic network in an updated form where information on white-tailed deer harvest regulations has been incorporated into the model (e.g. Regulations=Not In Effect; gray box) to evaluate the possible responses of the residual adult male population to the regulation at the local scale in Arkansas. Values associated with the histogram bars represent the probability that the parameter is in a particular state.

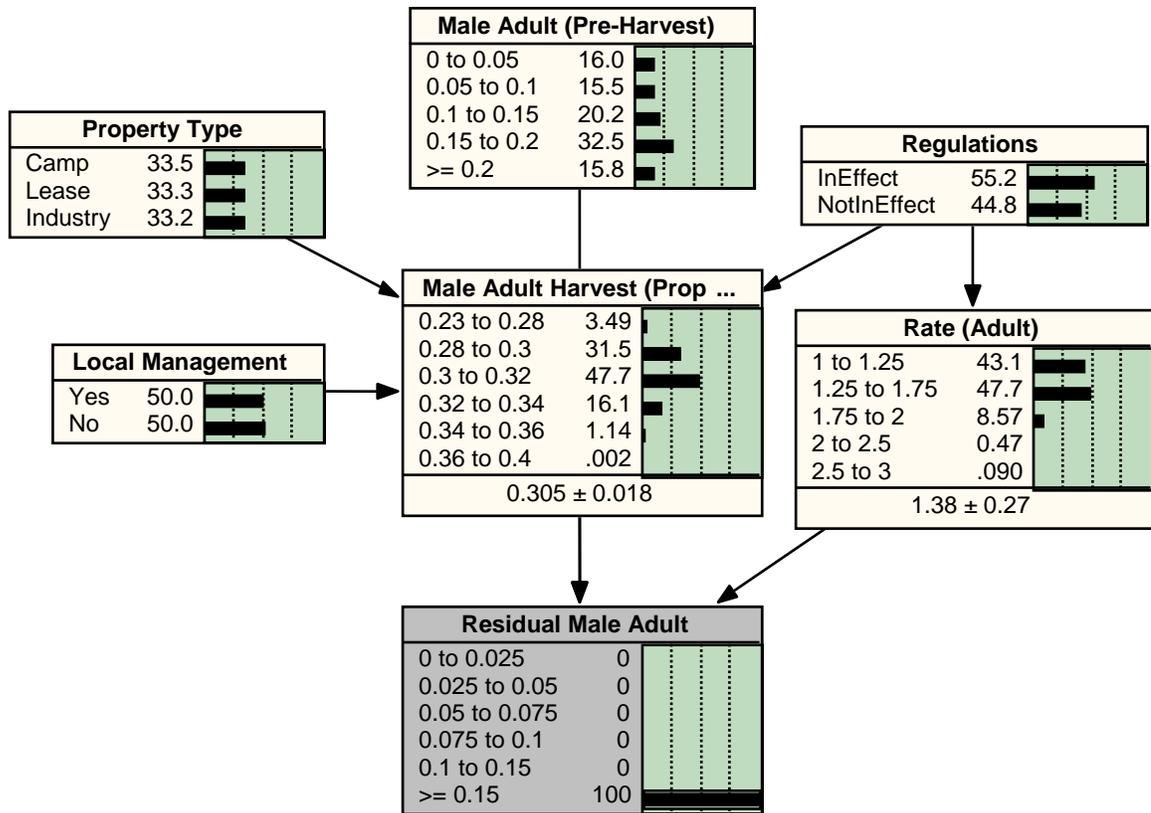


Fig. 15. Probabilistic network in an updated form where Bayesian updating was used in order to determine the ‘most likely’ states of model nodes given that the residual adult male age structure of the population is known and at a maximum (gray box) at the local scale in Arkansas. Values associated with the histogram bars represent the probability that the parameter is in a particular state.

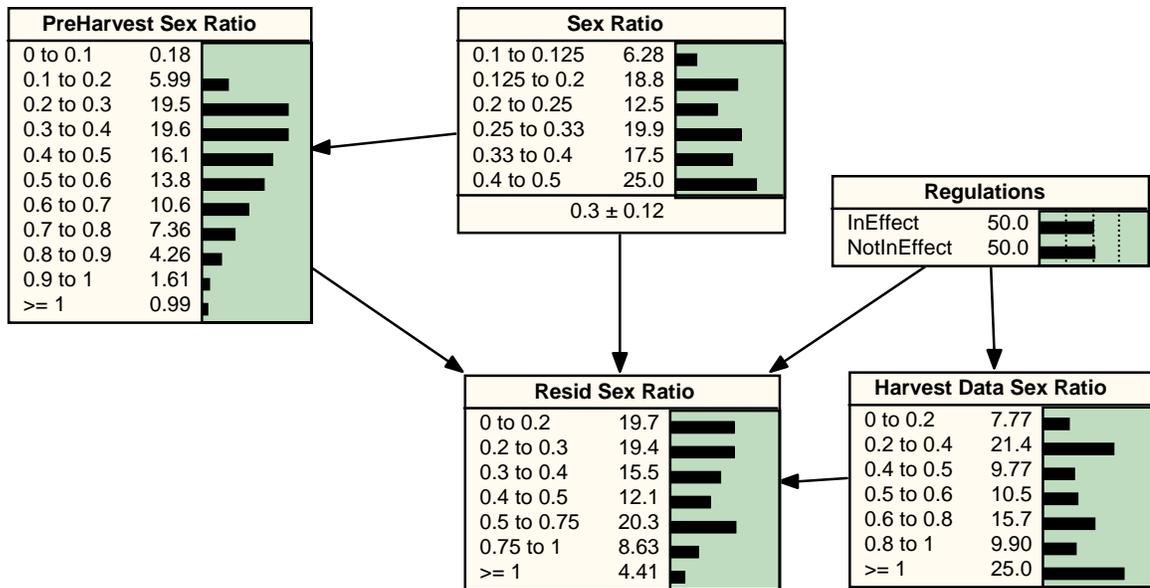


Fig. 16. This figure depicts a subset of probabilistic network in its initialized state based on output from the population model for evaluating the population response of residual population sex ratio at the local scale in Arkansas. Values associated with the histogram bars represent the probability that the parameter is in a particular state.

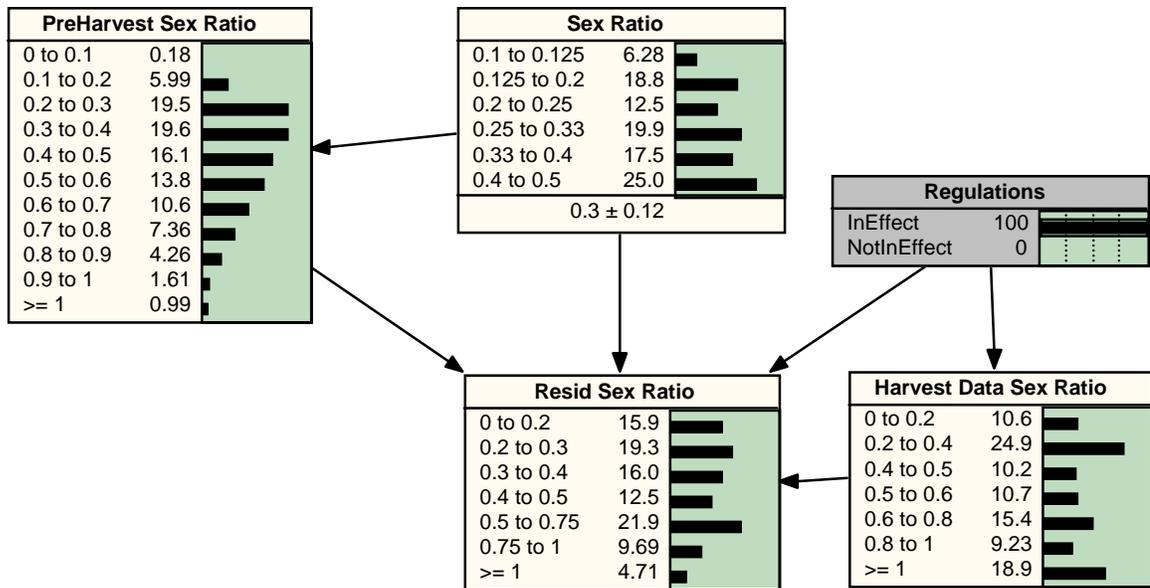


Fig. 17. Probabilistic network in an updated form where information on white-tailed deer harvest regulations has been incorporated into the model (e.g. Regulations=In Effect; gray box) to evaluate the possible responses of the residual population sex ratio to the regulation at the local scale in Arkansas. Values associated with the histogram bars represent the probability that the parameter is in a particular state.

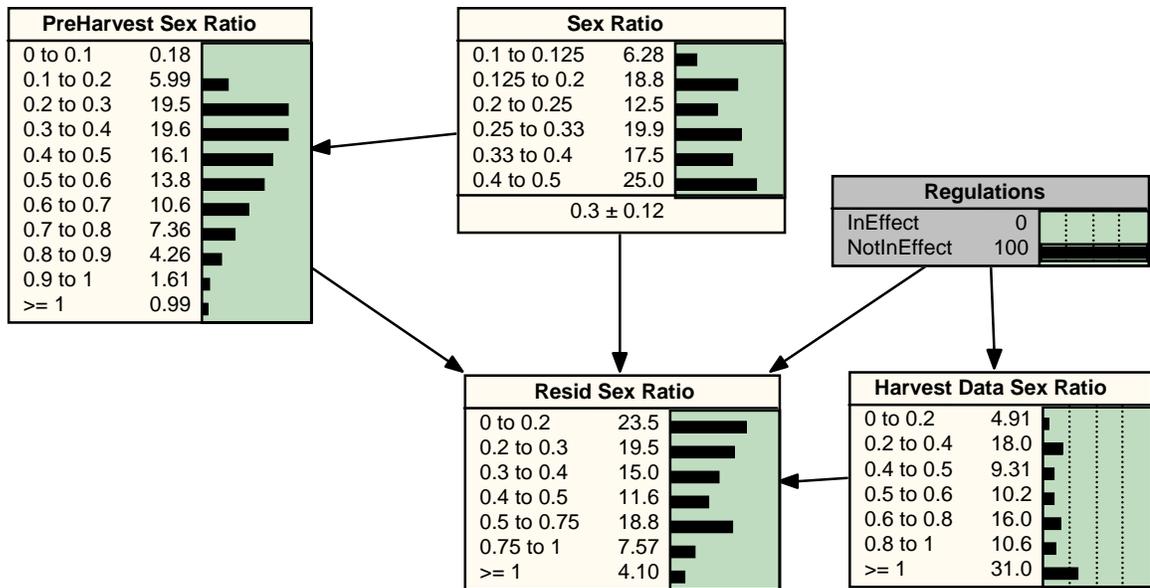


Fig. 18. Probabilistic network in an updated form where information on white-tailed deer harvest regulations has been incorporated into the model (e.g. Regulations=Not In Effect; gray box) to evaluate the possible responses of the residual population sex ratio to the regulation at the local scale in Arkansas. Values associated with the histogram bars represent the probability that the parameter is in a particular state.

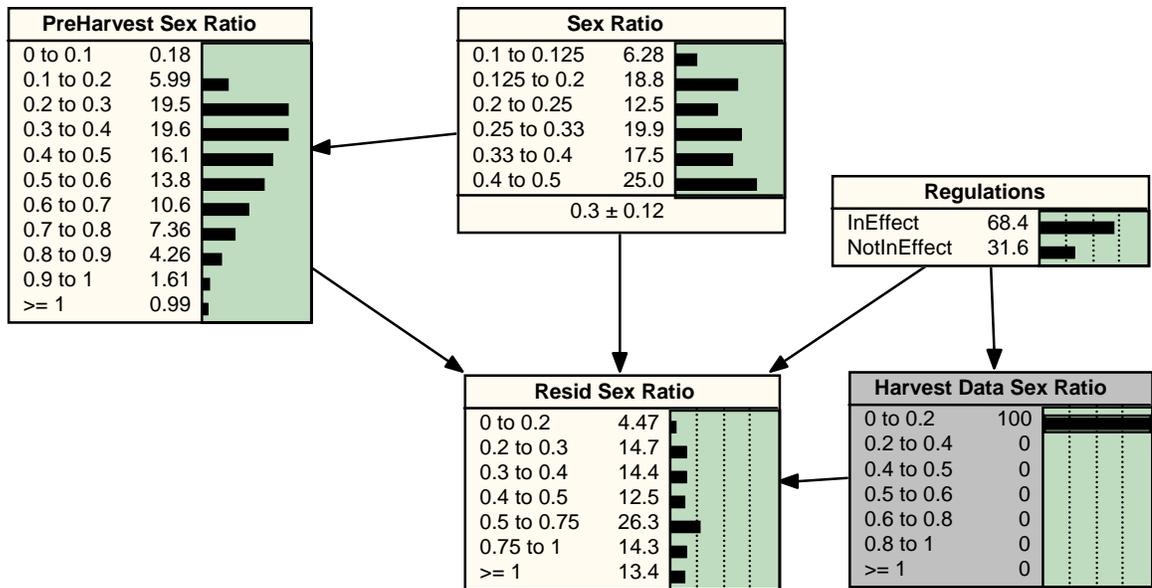


Fig. 19. Probabilistic network in an updated form where information on white-tailed deer harvest sex ratio has been incorporated into the model (e.g. Harvest Data Sex Ratio ≤ 0.2 ; gray box) to evaluate the possible responses of the residual population sex ratio to the regulation at the local scale in Arkansas. Values associated with the histogram bars represent the probability that the parameter is in a particular state.

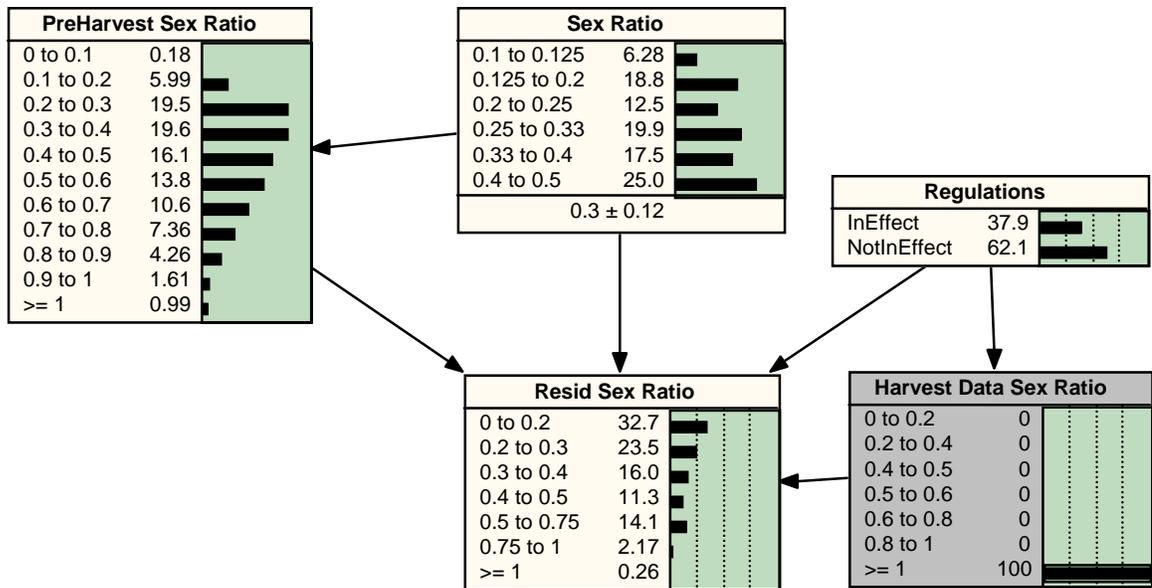


Fig. 20. Probabilistic network in an updated form where information on white-tailed deer harvest sex ratio has been incorporated into the model (e.g. Harvest Data Sex Ratio ≥ 1 ; gray box) to evaluate the possible responses of the residual population sex ratio to the regulation at the local scale in Arkansas. Values associated with the histogram bars represent the probability that the parameter is in a particular state.

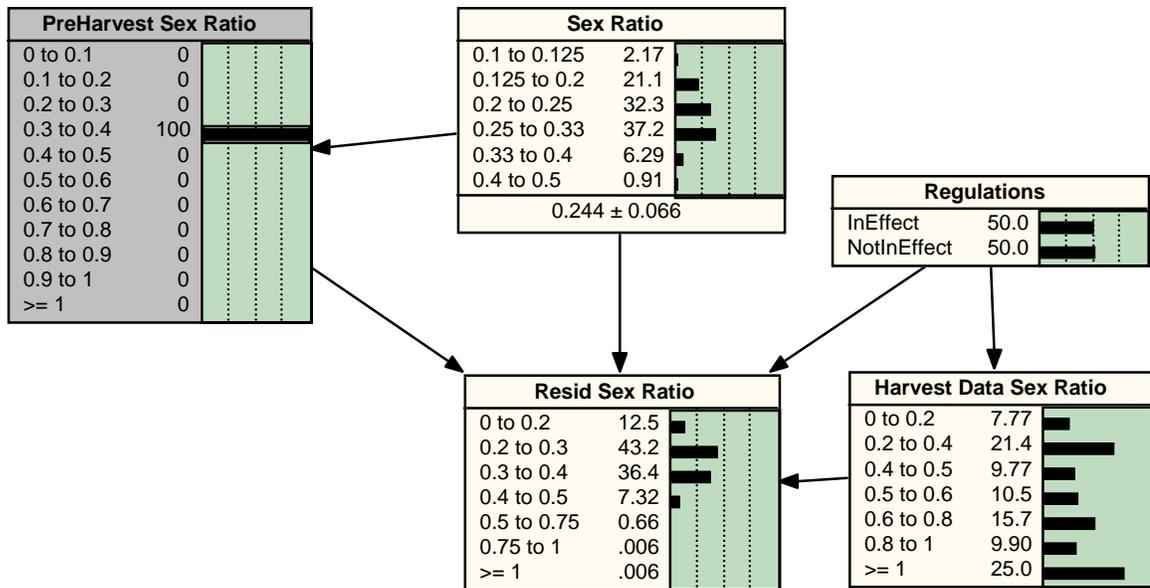


Fig. 21. Probabilistic network in an updated form where information on white-tailed deer pre-harvest sex ratio has been incorporated into the model (e.g. PreHarvest Sex Ratio 0.3 to 0.4; gray box) to evaluate the possible responses of the residual population sex ratio to the regulation at the local scale in Arkansas. Values associated with the histogram bars represent the probability that the parameter is in a particular state.

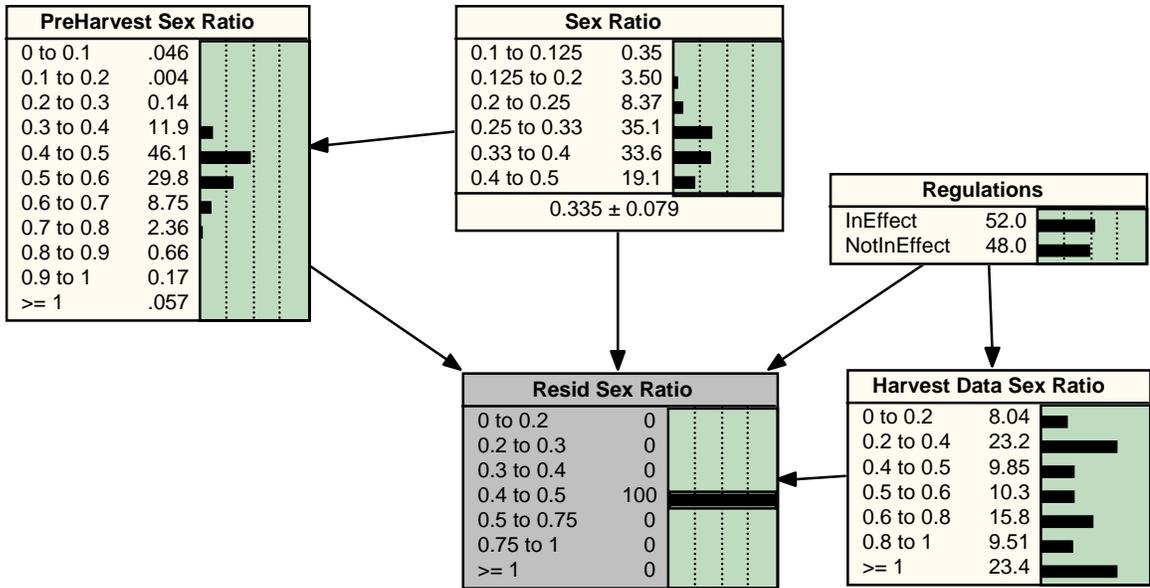


Fig. 22. Probabilistic network in an updated form where Bayesian updating was used in order to determine the ‘most likely’ states of model nodes given that the residual population sex ratio is known (0.4 to 0.5) (gray box) at the local scale in Arkansas. Values associated with the histogram bars represent the probability that the parameter is in a particular state.

APPENDIX 1

FINAL REPORT

State: Arkansas

Project Title

Impacts of Private and Public Land Management Strategies on White-Tailed Deer (*Odocoileus virginianus*) Management in Arkansas.

Period Covered: 1 July 2000 – 30 July 2004

Study Title

Impacts of Harvest Management on the Age and Sex Structure of White-Tailed Deer (*Odocoileus virginianus*) Populations in Arkansas.

Study Objectives

- (1) Determine what expectations private landowners/operators have regarding white-tailed deer management and planning by the Arkansas Game and Fish Commission (AGFC).
- (2) Evaluate and compare current land use and management practices used by private landowners/operators and the AGFC and evaluate what effects these practices have on local and regional white-tailed deer herd and harvest structure.

PRINCIPLE INVESTIGATOR: Dr. DAVID G. KREMENTZ

RESEARCH ASSISTANT: BRET A. COLLIER

RESEARCH OBJECTIVE 1A

To address objective 1, evaluate expectations, preferences, and opinions of landowner/operators towards white-tailed deer management and planning by the AGFC, we conducted 2 separate human dimensions surveys. The first survey was developed to evaluate white-tailed deer harvest and habitat management practices in use on white-tailed deer hunting camps registered in the Arkansas Deer Camp Programs (DCP). Our objective for this survey was to 1) provide baseline information to enable the AGFC to track and evaluate hunting camp participation in the Arkansas DCP, 2) provide an assessment of harvest and habitat management practices in use by hunting camps registered in the Arkansas DCP, 3) determine DCP participant's level of interest in AGFC management assistance programs and white-tailed deer management information, 4) identify and evaluate differences in implementation of harvest and habitat management practices by DCP participants, and 5) identify possible program actions for the AGFC to assist hunting camps on private lands with white-tailed deer management.

Final Report

In October 2003, a final project report titled "White-Tailed Deer Management on Private Lands in Arkansas" was delivered to the Arkansas Game and Fish Commission.

Research Summary

In September 2000, we mailed a questionnaire to hunt camp contacts for each white-tailed deer hunt camp registered in the Arkansas DCP (n=3,189). A second mailing was sent to all non-respondents 4 weeks later. A follow-up evaluating non-

response bias was not conducted. The response rate adjusted for non-deliverable surveys was 38% (1,184 responding hunt camps). Camp contacts were asked to provide information on: 1) their classification (land owner, land manager, camp manager), 2) location and acreage of hunt camp, 3) property type of hunt camp, 4) hunt camp management objective (if under Quality Deer Management (QDM) strategy), and 5) whether their hunt camp managed for wildlife species other than white-tailed deer. We asked respondents to rank 1) harvest management practices in excess of state regulations in use on hunt camp property, 2) habitat management practices in use on hunt camp property (both type and length of time), 3) types of AGFC provided management assistance that would benefit their hunt camp, 4) opinions on future AGFC management options, and 5) opinions on problems affecting their hunt camp. Respondents were asked: 1) to rate their level of interest in AGFC provided information on white-tailed deer management, 2) to rate which delivery method provided the most value, 3) to provide information on biological data collection, 4) whether their hunt camp worked with an AGFC biologist, and 5) whether their hunt camp would benefit from increased AGFC management assistance.

Executive Summary

- Hunt camps encompassed ~ 1.75 million acres of land in Arkansas
- Hunt camps average member size varied from a low of 13 (SE = 0.88) in the Ozarks to a high of 23 (SE = 3.15) in the Ouachitas.
- About 60% of hunt camps in Arkansas restricted white-tailed deer harvests to meet their specific management goals, regardless of statewide management goals.

- Across Arkansas, 40% of responding camps were under a QDM program.
- The primary management objective (61%) of hunt camps under QDM was to improve antler development/physical condition of the deer herd (deer harvest restricted to allow more bucks to reach older age classes of ≥ 2.5 years old).
- Across Arkansas, harvest management strategies in excess of state regulations used most frequently were restricted antlerless harvest (no button bucks) and minimum four (4)-point rule.
- Across Arkansas, 70% of hunt camps used winter food plots as their primary habitat management practice, while 60% and 50% of hunt camps also used supplemental feeding and supplemental minerals, respectively.
- 50% of hunt camps actively conducted habitat management for wildlife other than white-tailed deer.
- Across Arkansas, 57% of hunt camps stated that they had seen an increase in the number of bucks > 2.5 years old on their deer camps since they began using harvest and habitat management practices on their property.
- Across Arkansas, 77% of hunt camps stated that they had not seen an increase in the number of > 4.5 years old on their deer camps since they began using harvest and habitat management practices on their property.
- Across Arkansas, 65% felt that they did not have a more equal ratio of bucks to does on their deer camps property on their deer camps since they began using harvest and habitat management practices on their property.

- Across Arkansas, 56% of hunt camps felt that the management assistance program that would most benefit/interest their hunt camp was recommendations from a wildlife biologist.
- Across Arkansas, hunt camps felt that expanding educational efforts for hunters and hunt camps on deer management assistance for private lands was the most important future management option for the AGFC.

Because much of Arkansas is privately owned, the AGFC needs information regarding white-tailed deer management on private lands. This study provides the AGFC with an evaluation of hunt camp harvest and habitat management practices on a sample of private lands in Arkansas. Any comprehensive statewide management plan for white-tailed deer must provide for practices in use on private lands.

Citation

Collier, B. A., and D. G. Krementz. 2003. White-tailed deer management on private lands in Arkansas. Arkansas Cooperative Fish and Wildlife Research Unit Technical Report.

RESEARCH OBJECTIVE 1B

To address objective 1, we also evaluated expectations, preferences, and opinions of white-tailed deer hunters in Arkansas towards white-tailed deer management and planning by the AGFC, we conducted a 2nd separate human dimensions surveys. The 2nd survey was developed to evaluate white-tailed hunters opinions, preferences, and attitudes towards white-tailed deer management in Arkansas. Our objective for this survey was to 1) provide baseline information to enable the AGFC to track and evaluate white-tailed deer hunter opinions, preferences, and attitudes, 2) assess the level and type of white-tailed deer harvest that most interests/benefits hunters in Arkansas, 3) evaluate hunter opinions regarding state white-tailed deer harvest regulations, 4) evaluate hunter opinions regarding future white-tailed deer management options and goals, and 5) determine white-tailed deer hunter's level of interest in AGFC management assistance programs and deer management information.

Final Report

In January 2004, a final project report titled "Opinions, Preferences, and Attitudes of Hunters on White-Tailed Deer Management in Arkansas " was delivered to the Arkansas Game and Fish Commission.

Research Summary

In June 2001, we conducted a pilot study to: 1) test our sampling methodology, and 2) test the structure and format of the questionnaire. We sent an 8 page self-administered mail-back questionnaire (Appendix 1) to a randomly selected sample of

individuals who had purchased an Arkansas hunting license during 2000 (n=7,500). A second mailing was sent to all non-respondents 4 weeks later. A follow-up survey evaluating non-response bias was not conducted for the pilot study. Based on results and feedback from the pilot study conducted in 2001, we re-evaluated several questions before initiating the 2002 survey. In June 2002, we sent an 8 page self-administered mail-back questionnaire (Appendix 2) to a randomly selected sample of individuals who had purchased an Arkansas hunting license during 2001 (n=15,000). Two follow-up mailings were sent to all non-respondents at 3-week intervals. We evaluated non-response bias using a 2 page self-administered mail-back questionnaire in September 2002 (n=200, approximately 2% of non-respondents). Our adjusted response rate for the pilot and primary surveys were 35% (2,592) and 37% (5,496), respectively.

Hunters were asked to provide information on: 1) classification of primary property type hunted (club member (hunter on property involved in the Deer Camp Program (DCP)), hunter on public property, or hunter on private property (non-DCP)), 2) whether they hunted white-tailed deer in Arkansas, 3) length of time (years) hunting white-tailed deer (total and in Arkansas), 4) location of property hunted (county), and 5) hunting frequency, techniques, and methods used. We asked hunters to rank: 1) game species other than white-tailed deer actively hunted, 2) opinions on future results from the AGFC deer management plan, and 3) opinions on future AGFC management options. Hunters were asked to rate: 1) the importance of various harvest levels for an enjoyable season, 2) their opinions on what constituted a quality deer, 3) their opinions on management practices to increase opportunities to harvest a quality deer, and 4) which

types of deer management information would most interest them, as well as basic demographic information.

Executive Summary

- A majority of respondents (82%) stated that they hunted white-tailed deer in Arkansas.
- Most respondents (73%) hunted on property that was not registered in the Arkansas Deer Camp Program.
- Across Arkansas, 76% of hunters ranked hunting from an elevated stand as the technique used most frequently.
- A majority of hunters (77%) used center-fire rifles as their primary weapon.
- Many respondents (66%) stated that ‘knowing that the opportunity exists to harvest a buck’ was an extremely important aspect of an enjoyable deer season.
- Across Arkansas, those species most actively hunted other than white-tailed deer were squirrels (49%), turkeys (39%), waterfowl (36%), and rabbits (19%).
- Forty-five percent of hunters most frequently defined a quality deer as a healthy buck with >10 points, while 30% and 26%, respectively, defined a quality deer as a healthy doe, or a healthy buck with >8 points.
- About half of the hunters (51%) felt it was very likely that the 3-point rule would increase their opportunity to harvest a quality deer.
- Across Arkansas, 37% of hunters ranked restricted antlerless harvest (no button bucks) as the most beneficial practice to increase their opportunity to harvest a quality deer, while 29% ranked mandatory doe harvest as most beneficial.

- Only 38% of hunters ranked improving antler development / physical condition of the deer herd (harvest restricted to allow more bucks to reach >2.5 years old) as the most important result they would expect from the AGFC deer management plan.
- Across Arkansas, 29% of hunters ranked increasing antlerless hunting opportunities for the modern firearm season as the most important management option to increase herd quality.
- Other than information on hunting techniques, aging techniques, and prescribed burning, hunters were interested in all other information types.

This study provides the AGFC with an evaluation of hunter opinions, preferences, and attitudes regarding white-tailed deer management practices in Arkansas. Any comprehensive statewide management plan for white-tailed deer must provide for hunter opinions, preferences, and attitudes on current and future management practices.

Citation

Collier, B. A., and D. G. Kremetz. 2004. Opinions, preferences, and attitudes of hunters on white-tailed deer management in Arkansas. Arkansas Cooperative Fish and Wildlife Research Unit Technical Report.

RESEARCH OBJECTIVE 2¹

To address objective 2, we applied a new approach to management planning and evaluation of white-tailed deer population dynamics. Historical frameworks used by white-tailed deer managers when evaluating harvest management strategies and population goals are simplified approaches to a complex system. Therefore, a modeling approach is needed that allows for the combination of empirical and abstract population models for making quantitative assessments regarding white-tailed deer population responses to management actions. Limited demographic information across the range of white-tailed deer necessitates an approach that allows managers to incorporate what is known about white-tailed deer population dynamics with the effects of regulatory restrictions to assist in evaluating population response to management programs. Our approach allowed us to use a stochastic age and sex structured simulation model recast as a probabilistic model to 1) evaluate the affects of localized management and regulatory structure on white-tailed deer population dynamics, 2) evaluate uncertainty in parameter estimates and how uncertainty influences model predictions, and 3) evaluate the impact of regulatory restrictions as spatial scales increases, and 4) show how probabilistic modeling can assist agencies when planning management programs. The research results for RESEARCH OBJECTIVE 2 are outlined in Chapters 2 and 3 of this dissertation.

¹ Due to the extensive size and various levels of parameterization, underlying mathematics, and model structure, we refer the reader to dissertation chapters II - III.

Local scale simulation code (Chapter II)

```
#LOCAL SCALE (DCP PROPERTIES) R-CODE
#STOCHASTIC AGE- AND SEX-STRUCTURED WHITE-TAILED DEER
SIMULATION MODEL PROGRAM
#WRITTEN BY BRET A. COLLIER: UNIVERSITY OF ARKANSAS
library(gregmisc)
write(c("// ~->[CASE-1]->~"), "outputfileheadername.txt")
write(c('sexratio', 'density', 'ha', 'nhat', 'fawnagem', 'yearagem', 'subadagem', 'adagem',
'fawnagef', 'yearagef', 'subadagef', 'adagef', 'sfawn', 'syear', 'ssub', 'sad', 'eventcur',
'fawnsurvival', 'ffawncur', 'fyearcur', 'fsubcur', 'fadcur', 'mfawncur', 'myearcur', 'msubcur',
'madcur', 'avgbirths', 'fawnperfemale', 'preffawn', 'prefyear', 'prefsub', 'prefad', 'premfawn',
'premyear', 'premsub', 'premad', 'mfawnharv', 'myearharv', 'msubharv', 'madharv',
'ffawnharv', 'fyearharv', 'fsubharv', 'fadharv', 'resffawn', 'resfyear', 'resfsub', 'resfad',
'resmfawn', 'resmyear', 'resmsub', 'resmad', 'residsexratio', 'proptype', 'localmgt', 'regs',
'ratefawn', 'rateyear', 'ratesub', 'ratead', 'sr', 'resnhat'), "outputfilemainname")
write(c('nhat', 'fawnagem', 'yearagem', 'subadagem', 'adagem', 'fawnagef', 'yearagef',
'subadagef', 'adagef', 'fawnsurvival', 'ffawncur', 'fyearcur', 'fsubcur', 'fadcur', 'mfawncur',
'myearcur', 'msubcur', 'madcur', 'avgbirths', 'fawnperfemale', 'preffawn', 'prefyear',
'prefsub', 'prefad', 'premfawn', 'premyear', 'premsub', 'premad', 'mfawnharv', 'myearharv',
'msubharv', 'madharv', 'ffawnharv', 'fyearharv', 'fsubharv', 'fadharv', 'resffawn', 'resfyear',
'resfsub', 'resfad', 'resmfawn', 'resmyear', 'resmsub', 'resmad', 'residsexratio',
'resnhat'), "outputfilesummaryname")
scennum<-c('one', 'two', 'three', 'four', 'five', 'six', 'seven', 'eight', 'nine', 'ten', 'eleven',
'twelve')
paste("c:/Documents and Settings/bacolli/Desktop/Dissertation/BBN Data (Local
MGT)/Data CSV/scen",scennum,"buck.csv", sep="")
paste("c:/Documents and Settings/bacolli/Desktop/Dissertation/BBN Data (Local
MGT)/Data CSV/scen",scennum,"doe.csv", sep="")
data<-vector("list", 12)
  for (i in seq(along=data)) {
data[[i]]<-list(male=read.csv(paste("c:/Documents and
Settings/bacolli/Desktop/Dissertation/BBN Data (Local MGT)/Data
CSV/scen",scennum,"buck.csv", sep="")),female=read.csv(paste("c:/Documents and
Settings/bacolli/Desktop/Dissertation/BBN Data (Local MGT)/Data
CSV/scen",scennum,"doe.csv", sep="")))
}
category <- matrix(c("Camp", "Yes", "InEffect", "Lease", "Yes", "InEffect", "Industry",
"Yes", "InEffect", "Camp", "Yes", "NotinEffect", "Lease", "Yes", "NotinEffect",
"Industry", "Yes", "NotinEffect", "Camp", "No", "InEffect", "Lease", "No", "InEffect",
"Industry", "No", "InEffect", "Camp", "No", "NotinEffect", "Lease", "No",
"NotinEffect", "Industry", "No", "NotinEffect"), byrow=T, nrow=12, ncol=3)

#-----
#START SIMULATION HERE
#set.seed(1001)
```

```

    for (simulation in 1:n) {
#-----
# INITIAL PARAMETER ESTIMATES
#-----
density <- round(runif(1, .15, .5 ), digits=2)
ha <- round(runif(1, 80, 1100))
n.hat <- round(density*ha)
sex.ratio <-round(runif(1, .1, .5), digits=4)
agem <- c(.40, .30, .15, .15)
age.structm <-round(rdirichlet(1, alpha=agem), digits=4)
agef <- c(.175, .175, .25, .40)
age.structf <-round(rdirichlet(1, alpha=agef), digits=4)
r <- round(rep(runif(2, c(.3, .7), c(.99, .99)),each=2), digits=4)
l <- c(.03, 1.22, 1.69, 1.78)
fs<-round(runif(1, .15, .85), digits=4)
i <- sample(1:12, 1)
    m<-data[[i]]$male
    f<-data[[i]]$female
    scenar<- category[i,]
alpha.prior <- rep(1, NCOL(m))
harv.mp<- round(rdirichlet(1, alpha=alpha.prior+colSums(m)), digits=4)
alpha.prior <- rep(1, NCOL(f))
harv.fp<- round(rdirichlet(1, alpha=alpha.prior+colSums(f)), digits=4)
rate <- if (i <=3) rep(runif(2, c(.25, 1), c(.75, 2)), each=2) else
    if (i <=6) rep(runif(2, c(.5, 1), c(1.5, 2)), each=2) else
    if (i <=9) rep(runif(2, c(.25, 1), c(1.25, 2)), each=2)else
    if (i <=12)rep(runif(2, c(.75, 1), c(2, 3)), each=2)
rate <- round(rate, digits=4)
harv.m <- harv.mp*rate
harv.m <- pmin(harv.m,1)
harv.m <- round(harv.m, digits=4)
ep <-event.post <-rbinom(1, 1, 0.1)
dumep <-ep
#SET UP 20 YEAR SIMULATIONS HERE
    for (simnum in 1:20) {
#-----
#Set Beginning Population
#-----
ec <-event.current <- rbinom(1, 1, 0.1)
ep <-dumep
    dumec <-ec
        popln.male<- n.hat*sex.ratio
        popln.female<- n.hat*(1-sex.ratio)
        popln.m.age<- round(popln.male*age.structm)
        popln.f.age<- round(popln.female*age.structf)
#-----

```

```

#Set Current Population Parameters
#-----
if (simnum == 1) popln.m.age == popln.m.age
if (simnum == 1) popln.f.age == popln.f.age
if (simnum > 1) popln.m.age == residual.pop[,1]
if (simnum > 1) popln.f.age == residual.pop[,2]
n.female.surv <- sapply(lapply(1:4, function(i) sample(x=c(1,0), replace=T,
size=popln.f.age[i], prob=c(r[i], 1-r[i])))), sum)
n.male.surv <- sapply(lapply(1:4, function(i) sample(x=c(1,0), replace=T,
size=popln.m.age[i], prob=c(r[i], 1-r[i])))), sum)
total.surv <- sum(n.male.surv, n.female.surv)
popln.m.vector <- n.male.surv/total.surv
popln.f.vector <- n.female.surv/total.surv
popln.m.vector <- round((popln.m.vector), digits=2)
popln.f.vector <- round((popln.f.vector), digits=2)
#-----
#Birth-Recruitment-Transition Processes
#-----
#Overall recruitment
d <- if(ec) fs*(runif(1, .25, .75)) else fs
d <- round((d), digits=4)
recruit.f <- n.female.surv
x <- sum(unlist(lapply(seq(along=1), function(i)
sample(0:2,recruit.f[i],replace=T,prob=dpois(0:2,l[i])))))
avg.births <- round((sum(x)/sum(n.female.surv)), digits=4)
z <- sapply(lapply(1, function(i) sample(x=c(1,0), replace=T, size=x, prob=c(d,1-d)),
sum)
z <- sum(z)
fawn.per.female <-round((z/sum(n.female.surv)), digits=4)
#Separate Recruitment by Sex
sr <- if(ep) round(runif(1, .5, .65), digits=4) else round(runif(1, .3, .5), digits=4)
new.female <- round(z*(1-sr))
new.male <- round(z*sr)
#Include Transition Here Recuit->F, F->Y, Y->S, S->A
f.old <- n.female.surv
f.old[3] <- f.old[3] + f.old[4]
current.female <- c(new.female, f.old[1:3])
m.old <- n.male.surv
m.old[3] <-m.old[3]+ m.old[4]
current.male <- c(new.male, m.old[1:3])
#Pull Transitions Together
preharv.pop <- sum(current.female, current.male)
preharvest.male <- round((current.male/preharv.pop), digits=4)
preharvest.female <- round((current.female/preharv.pop), digits=4)
#-----
#Harvest Implementation

```

```

#-----
curr.fem <- current.female
  harv.fem <- sapply(lapply(1:4, function(i) sample(x=c(0,1), replace=T,
size=curr.fem[i], prob=c(harv.fp[i], 1-harv.fp[i]))), sum)
curr.male <- current.male
  harv.male <- sapply(lapply(1:4, function(i) sample(x=c(0,1), replace=T,
size=curr.male[i], prob=c(harv.m[i], 1-harv.m[i]))), sum)
resid.fem <- harv.fem
resid.male <- harv.male
residual.pop <- cbind(resid.male, resid.fem)
#-----
#Output Population Structure Estimates for BBN
#-----
resid.pop.male <-sum(harv.male)
resid.pop.female <-sum(harv.fem)
resid.pop <- sum(resid.fem, resid.male)
resid.m.vector <- round((resid.male/resid.pop), digits=4)
resid.f.vector <- round((resid.fem/resid.pop), digits=4)
#Output Sex Ratio
resid.sexratio <- round((resid.pop.male/resid.pop.female), digits=4)
dumep <- dumec
#HERE WOULD ALSO BE NICE TO WRITE CODE TO PLOT POPLN RESPONSE
BY AGE CLASS FOR 20 YEARS
#END 20 YEAR SIMULATION HERE
}
write(c(sex.ratio, density, ha, n.hat, age.structm, age.structf, r, ec, d, popln.f.vector,
popln.m.vector, avg.births, fawn.per.female, preharvest.female, preharvest.male,
harv.mp, harv.fp, resid.f.vector, resid.m.vector, resid.sexratio, scenar, rate, sr, resid.pop),
"outputfilemainname")
write(c(n.hat, age.structm, age.structf, d, popln.f.vector, popln.m.vector, avg.births,
fawn.per.female, preharvest.female, preharvest.male, harv.mp, harv.fp, resid.f.vector,
resid.m.vector, resid.sexratio, resid.pop), "outputfilessummaryname")
#END OVERALL SIMULATION HERE
}

```

Spatial scale simulation code (Chapter II)

```
#SPATIAL SCALE R-CODE
#STOCHASTIC AGE- AND SEX-STRUCTURED WHITE-TAILED DEER
SIMULATION MODEL PROGRAM
#WRITTEN BY BRET A. COLLIER: UNIVERSITY OF ARKANSAS
#PH.D. DISSERTATION RESEARCH
library(gregmisc)
data<- read.csv("inputdata.txt")
write(c("//~>[CASE-1]->~"), "outputheaderfile.txt")
write(c('density', 'sexratio', 'nhat', 'fawnagem', 'yearagem', 'subagem', 'adagem',
'fawnagef', 'yearagef', 'subagef', 'adagef', 'sfawn', 'syear', 'ssub', 'sad', 'fawnsurvival',
'eventcur', 'mfawncur', 'myearcur', 'msubcur', 'madcur', 'ffawncur', 'fyearcur', 'fsubcur',
'fadcur', 'avgbirths', 'fawnperfemale', 'sr', 'premfawn', 'premyear', 'premsub', 'premad',
'preffawn', 'prefyear', 'prefsub', 'prefad', 'mfawnharv', 'myearharv', 'msubharv', 'madharv',
'ffawnharv', 'fyearharv', 'fsubharv', 'fadharv', 'residmfawn', 'residmyear', 'residmsub',
'residmad', 'residffawn', 'residfyear', 'residfsub', 'residfad', 'residsexratio', 'regs', 'county',
'region', 'poh', 'pagri', 'ppine', 'countysize', 'ratemfawn', 'ratemyear', 'ratemsub', 'ratemad',
'rateffawn', 'ratefyear', 'ratefsub', 'ratefad', 'poachfawn', 'poachyear', 'poachsub', 'poachad',
'residnhat'), "outputdatasetmain")
write(c('density', 'nhat', 'fawnagem', 'yearagem', 'subagem', 'adagem', 'fawnagef',
'yearagef', 'subagef', 'adagef', 'fawnsurvival', 'mfawncur', 'myearcur', 'msubcur', 'madcur',
'ffawncur', 'fyearcur', 'fsubcur', 'fadcur', 'avgbirths', 'fawnperfemale', 'premfawn',
'premyear', 'premsub', 'premad', 'preffawn', 'prefyear', 'prefsub', 'prefad', 'mfawnharv',
'myearharv', 'msubharv', 'madharv', 'ffawnharv', 'fyearharv', 'fsubharv', 'fadharv',
'residmfawn', 'residmyear', 'residmsub', 'residmad', 'residffawn', 'residfyear', 'residfsub',
'residfad', 'residsexratio', 'regs', 'county', 'region', 'poh', 'pagri', 'ppine', 'countysize',
'residnhat'), "outputdatasetsummary")

#-----
#START SIMULATION HERE
  for (simulation in 1:n) {
#-----
#SCALE SELECTION (COUNTY WITHIN REGION)
#-----
exclude <- c(grep("Sex",names(data)),grep("Season", names(data)),
grep("AGE.0.5",names(data)), grep("AGE.1.5",names(data)),
grep("AGE.2.5",names(data)), grep("AGE.3.5",names(data)))
data.code <- apply(apply(data[,-exclude], 2, as.character), 1, paste, collapse=":")
this.one <- sample(unique(data.code), s=1)
ind <- which(data.code==this.one)
location.code <- unlist(strsplit(this.one, ":"))#splits up the concatenated vector so it
deals with UNLIST for output and if (Region==)
# Initial Abundance
density<- if (location.code[3]=="1") rpois(1, 5) else
  if (location.code[3]=="2") rpois(1, 7) else
```

```

    if (location.code[3]=="3") rpois(1, 3) else
    if (location.code[3]=="4") rpois(1, 10)
density <- pmax(density, 2)
#PROPORTIONAL HABITAT RELATIONSHIP
size <-as.numeric(location.code[7])
max.deer <-density*size
k <-max.deer
poh <-as.numeric(location.code[4])*1
ppine <- as.numeric(location.code[5])* .85
pagri <- as.numeric(location.code[6])* .4
n.oh <-max.deer*poh
n.pine <-max.deer*ppine
n.agri <- max.deer*pagri
#-----
#INITIAL PARAMETER ESTIMATES
#-----
n.hat <- round(sum(n.oh, n.pine, n.agri))
sex.ratio <-round(runif(1, .1, .5), digits=4)
agem <- c(.50, .30, .15, .05)
age.structm <-round(rdirichlet(1, alpha=agem), digits=3)
agef <- c(.125, .125, .25, .50) #data from AGFC
age.structf <-round(rdirichlet(1, alpha=agef), digits=3)
r <- round(rep(runif(2, c(.3, .7), c(.99, .99)), each=2), digits=3)
l <- if (location.code[3]=="1") c(0, 0.83, 1.92, 1.86) else
    if (location.code[3]=="2") c(0, 1.11, 1.4, 1.54) else
    if (location.code[3]=="3") c(0.05, 0.82, 1.53, 1.78) else
    if (location.code[3]=="4") c(0, 0.58, 1.12, 1.69)
js<-round(rnorm(1, 0.5, .1), digits=3)
#-----
#HARVEST DATA SETUP
#-----
mf <- data[intersect(ind,which(data$Sex=="Buck")),grep("AGE.0.5",names(data))]
my <- data[intersect(ind,which(data$Sex=="Buck")),grep("AGE.1.5",names(data))]
ms <- data[intersect(ind,which(data$Sex=="Buck")),grep("AGE.2.5",names(data))]
ma <- data[intersect(ind,which(data$Sex=="Buck")),grep("AGE.3.5",names(data))]
m <- as.matrix(cbind(mf, my, ms, ma))
ff <- data[intersect(ind,which(data$Sex=="Doe")),grep("AGE.0.5",names(data))]
fy <- data[intersect(ind,which(data$Sex=="Doe")),grep("AGE.1.5",names(data))]
fs <- data[intersect(ind,which(data$Sex=="Doe")),grep("AGE.2.5",names(data))]
fa <- data[intersect(ind,which(data$Sex=="Doe")),grep("AGE.3.5",names(data))]
f <- as.matrix(cbind(ff, fy, fs, fa))
default.f <-matrix(c(5950, 7931, 10223, 6737), nrow=1)# For LMAV ONLY
f <- if (NROW(f)==0) default.f else f
alpha.prior <- rep(1, NCOL(m))
harv.mp<- round(rdirichlet(1, alpha=alpha.prior+colSums(m)), digits=3)
alpha.prior <- rep(1, NCOL(f))

```

```

harv.fp<- round(rdirichlet(1, alpha=alpha.prior+colSums(f)), digits=3)
rate.m <- if (location.code[1]=="1") rep(runif(2, c(.75, 1), c(2, 2)), each=2) else
  if (location.code[1]=="2") rep(runif(2, c(.25, 1), c(1.25, 2)), each=2)
rate.f <- if (location.code[1]=="1") rep(runif(2, c(.25, .5), c(1, 1)), each=2) else
  if (location.code[1]=="2") rep(runif(2, c(.5, 1), c(1.5, 2)), each=2)
harv.m <- harv.mp*rate.m
harv.f <- harv.fp*rate.f
harv.m <- pmin(harv.m,1)
harv.f <-pmin(harv.f, 1)
harv.m <- round(harv.m, digits=3)
harv.f <-round(harv.f, digits=3)
poach <-rep(runif(2, c(0, 0), c(0.15, 0.3)), each=2)
ep <-event.post <-rbinom(1, 1, 0.1)
dumep <-ep
resid.pop <- n.hat
#SET UP 20 YEAR SIMULATIONS HERE
  for (simnum in 1:20) {
#-----
#Set Beginning Population
#-----
ec <-event.current <- rbinom(1, 1, 0.1)
ep<-dumep
dumec <-ec
      popln.male<- n.hat*sex.ratio
      popln.female<- n.hat*(1-sex.ratio)
      popln.m.age<- round(popln.male*age.structm)
      popln.f.age<- round(popln.female*age.structf)
#-----
#Set Current Population Parameters
#-----
if (simnum == 1) popln.m.age == popln.m.age
if (simnum == 1) popln.f.age == popln.f.age
if (simnum > 1) popln.m.age == resid.m.poach
if (simnum > 1) popln.f.age == resid.f.poach
n.female.surv <- sapply(lapply(1:4, function(i) sample(x=c(1,0), replace=T,
size=popln.f.age[i], prob=c(r[i], 1-r[i]))), sum)
n.male.surv <- sapply(lapply(1:4, function(i) sample(x=c(1,0), replace=T,
size=popln.m.age[i], prob=c(r[i], 1-r[i]))), sum)
total.surv <- sum(n.male.surv, n.female.surv)
popln.m.vector <- round((n.male.surv/total.surv), digits=2)
popln.f.vector <- round((n.female.surv/total.surv), digits=2)
#-----
#Birth-Recruitment-Transition Processes
#-----
recruit.f <- n.female.surv

```

```

x <- sum(unlist(lapply(seq(along=1), function(i)
sample(0:2,recruit.f[i],replace=T,prob=dpois(0:2,l[i])))))
avg.births <- round((sum(x)/sum(n.female.surv)), digits=3)
d <- (js*(1-exp(-k/(total.surv + x)))^(total.surv/resid.pop)
d <- if (ec) d*(runif(1, .25, .75)) else d
d <- round((d), digits=3)
d <- pmin(d, 1)
z <- sapply(lapply(1, function(i) sample(x=c(1,0), replace=T, size=x, prob=c(d,1-d))),
sum)
z <- sum(z)
fawn.per.female <-round((z/sum(n.female.surv)), digits=3)
#Separate recruitment by sex
sr <- if(ep) round(runif(1, .5, .65), digits=3) else round(runif(1, .3, .5), digits=3)
new.female <- round(z*(1-sr))
new.male <- round(z*sr)
#Include transition here for Recruit->F, F->Y, Y->S, S->A
f.old <- n.female.surv
f.old[3] <- f.old[3] + f.old[4]
current.female <- c(new.female, f.old[1:3])
m.old <- n.male.surv
m.old[3] <-m.old[3]+ m.old[4]
current.male <- c(new.male, m.old[1:3])
#Pull transitions together
preharv.pop <-sum(current.female, current.male)
preharvest.male <-round((current.male/preharv.pop), digits=3)
preharvest.female <-round((current.female/preharv.pop), digits=3)
#-----
#Harvest Model Implementation
#-----
curr.fem <- current.female
harv.fem <- sapply(lapply(1:4, function(i) sample(x=c(0,1), replace=T,
size=curr.fem[i], prob=c(harv.f[i], 1-harv.f[i]))), sum)
curr.male <- current.male
harv.male <- sapply(lapply(1:4, function(i) sample(x=c(0,1), replace=T,
size=curr.male[i], prob=c(harv.m[i], 1-harv.m[i]))), sum)
resid.fem <- harv.fem
resid.male <- harv.male
#-----
#Output Population Structure Estimates for BBN
#-----
resid.m.poach <-sapply(lapply(1:4, function(i) sample(x=c(0, 1), replace=T,
size=resid.male[i], prob=c(poach[i], 1-poach[i]))), sum)
resid.f.poach <- sapply(lapply(1:4, function(i) sample(x=c(0, 1), replace=T,
size=resid.fem[i], prob=c(poach[i], 1-poach[i]))), sum)
resid.pop.male <- sum(resid.m.poach)
resid.pop.female <- sum(resid.f.poach)

```

```

resid.pop <- sum(resid.f.poach, resid.m.poach)
resid.m.vector <- round((resid.m.poach/resid.pop), digits=3)
resid.f.vector <- round((resid.f.poach/resid.pop), digits=3)
#Output Sex Ratio
resid.sexratio <- round((resid.pop.male/resid.pop.female), digits=3)
dumep <-dumec
#END 20 YEAR SIMULATION HERE
}
write(c(density, sex.ratio, n.hat, age.structm, age.structf, r, js, ec, popln.m.vector,
popln.f.vector, avg.births, fawn.per.female, sr, preharvest.male, preharvest.female,
harv.mp, harv.fp, resid.m.vector, resid.f.vector, resid.sexratio, location.code, rate.m,
rate.f, poach, resid.pop), "outfilemainname")
write(c(density, n.hat, age.structm, age.structf, js, popln.m.vector, popln.f.vector,
avg.births, fawn.per.female, preharvest.male, preharvest.female, harv.mp, harv.fp,
resid.m.vector, resid.f.vector, resid.sexratio, location.code, resid.pop),
"outputfilesummaryname")
#END OVERALL SIMULATION HERE
}

```

VITA

Bret Aaron Collier was born on 1 September 1973 in Mattoon, Illinois. Growing up in a rural area in east central Illinois, and being involved in his extended families agricultural practices at an early age he developed a keen interest in wildlife and the outdoors. After graduating from Mattoon Senior High School in 1991, he began studies at Eastern Illinois University.

While at Eastern Illinois University, Bret focused his undergraduate work in resource economics, where his interests were primarily in rural economies and agribusiness. He completed his Bachelors of Arts in Economics in 1997 from Eastern Illinois University. He then migrated south to Oklahoma State University to begin graduate work in Agricultural Economics focusing on natural resource and environmental economics.

While at Oklahoma State University, Bret served as a graduate teaching assistant in the Agricultural Economics department for a variety of courses, including Non-major's Agricultural Marketing, Major's Agricultural Policy, and Natural Resource and Environmental Economics. While at OSU, Bret conducted ancillary research projects with Dr. Larry Sanders on public opinion regarding property rights in conjunction with professors at Michigan State University. Bret began conducting research on cost-benefit analysis of hunters in Oklahoma. In 1997, he completed his Master of Science degree with the defense of his thesis: "White-tailed deer hunting in Oklahoma: An economic analysis of deer hunter preferences in 1998." In the summer of 1999, he moved east to begin his doctoral work in the Arkansas Cooperative Fish and Wildlife Research Unit, University of Arkansas under the advisement of Dr. David G. Krementz.

Bret served as a graduate assistant in the Arkansas Cooperative Fish and Wildlife Research Unit, as well as a teaching assistant for Principles of Biology Laboratory in the Department of Biological Sciences. His previous interests in human dimensions research and statistics allowed him to conduct several projects in addition to his dissertation research. The side projects included evaluation of management practices in use by white-tailed deer hunting camps in Arkansas, evaluation of white-tailed deer hunter opinions and preferences towards deer management in Arkansas, and estimation of timber rattlesnake (*Crotalus horridus*) survival rates in northwest Arkansas with Dr. Steve Beaupre and Dr. William Thompson. In addition to these projects, Bret successfully completed coursework required for a Master of Statistics, and in that capacity served as a statistical consultant for Biology department faculty and graduate students. Bret was a regular guest lecturer in the statistics department, lecturing in courses on sampling theory and bio-statistics, as well as coordinating a Bayesian statistics seminar. On 20 September 2004, he successfully defended his dissertation.

Bret is a member of The Wildlife Society, the American Statistical Association, International Biometrics Society, Institute of Mathematical Statistics, American Fisheries Society, and American Ornithologists Union. Over the course of his graduate student career, he has authored or co-authored 2 technical reports, 9 presentations at national meetings, and has 2 manuscripts under review with several with more in preparation

EVALUATING IMPACT OF SELECTIVE HARVEST MANAGEMENT ON AGE
STRUCTURE AND SEX RATIO OF WHITE-TAILED DEER (*Odocoileus virginianus*)
IN ARKANSAS

Abstract of dissertation submitted in partial fulfillment of the requirements for the degree
of Doctor of Philosophy

By

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Dissertation Director:

David G. Krementz

ABSTRACT

Harvest management is the primary tool used by white-tailed deer managers to manipulate population size and structure. I modeled white-tailed deer population response to alternative harvest management practices at multiple spatial scales to evaluate the impacts of parameter uncertainty on predictive ability across multiple spatial scales. I applied stochastic population modeling combined with probabilistic causal models to quantitatively evaluate and represent uncertainty in population response, as well as providing a tool for white-tailed deer adaptive management programs. Stochastic population modeling combined with probabilistic models suggests that at local scales, regulatory restrictions slightly increased residual male population age structure and residual population sex ratio. Sensitivity analysis indicates that male population response was most influenced by pre-harvest population structure, while residual population sex ratio was most sensitive to pre-harvest population sex ratio and initial sex ratio, none of which are data commonly collected by deer managers. Model predictions indicated that as spatial resolution declined, the antler restriction increased yearling recruitment into sub-adult age classes, however this shift was accompanied by increased estimate uncertainty. Model predictions show that benefits of protecting yearlings using antler restrictions were lost after age class transition due to excessive pressure on the sub-adult age class. Residual population sex ratio increased under current regulations, but was accompanied by an increase in variance. My approach represents a significant deviation from current methods used to evaluate white-tailed deer population responses to harvest management. Current approaches do not account for variation in underlying biological processes, and as such are influenced by considerable sources of bias and have little

relevancy for adequately evaluating management practices. Thus, an adaptive approach that clearly demonstrates where information is lacking and accounts for limited information through probabilistic representation of population responses represents a new application for management planning. Because accurate population parameter relationships are limited across a broad scale, probabilistic modeling provided a useful tool for biologically justifying management actions while explicitly dealing with parameter uncertainty.