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Survival analysis and computer simulations of lethal and contraceptive management strategies for urban deer

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Abstract: I monitored survival of 34 female white-tailed deer (*Odocoileus virginianus*) in Bloomington, Minnesota, from October 1996 to December 1999. Twenty deer died: nineteen were killed by vehicles, and one was killed in a deer-removal program conducted by an adjacent suburb. Summer survival was high and varied little over the 3 years of study (range = 0.93 to 0.95). Fall survival ranged from 0.84 to 1.00, and winter survival was generally high during the 3 years of study, except during a severe winter (range = 0.72 to 0.95). I calculated population growth rates (λ) from Leslie matrix projections, using these survival estimates and productivity data collected from road-killed female deer in the Twin Cities (Minneapolis-St. Paul, Minnesota, USA) metropolitan area. When winter survival was high (0.94), my model simulations indicated the Bloomington deer population increased by 21% when no deer management program was in place. When a low winter survival rate (0.72) was modeled, the population decreased by 7%, even when no deer management program was implemented. I modeled what impact contraception may have on population growth and concluded that treating >50% of adult female deer was necessary to stabilize population growth, and treating all females was necessary to decrease population growth under high winter survival conditions. I concluded that removal programs are more effective than immunocontraception programs because survival contributes more to population growth rates in deer populations than fecundity. I recommend removing 20% and 40% of adult female deer in the population to cause the population to stabilize or to reduce deer numbers, respectively. I recommend managers collect deer–vehicle collision data because these data potentially represent the most accurate and easily-obtainable life history component of an urban deer herd.

Key words: contraception, human–wildlife conflicts, management strategies, population modeling, survival, urban

White-tailed deer (*Odocoileus virginianus*) are common in many urban areas across the United States. Urban deer typically bring about unique management situations for wildlife managers because opinions of residents regarding management options for deer generally vary and oftentimes conflict. While traditional measures to manage deer have proven effective (McAninch and Parker 1991, Ver Steeg et al. 1995, McDonald et al. 2007, DeNicola and Williams 2008), some residents will not support lethal management programs (Cornicelli 1992) and usually favor nonlethal management strategies (Curtis et al. 1995). One such nonlethal management option is gonadotropin-releasing hormone contraception (Miller et al. 2009), which soon may be available as a legitimate management option for urban communities to use (Fagerstone et al. 2008).

A major challenge exists for wildlife managers to develop useful, predictive models that can evaluate how various urban deer management strategies will affect population growth. Although estimates of survival have been reported from deer occupying rural landscapes (Nelson and Mech 1986, Nixon et al. 1991, Van Deelan et al. 1997), survival studies conducted with urban deer have received scant attention. Empirical data could improve predictive models for urban deer. My objectives were to estimate seasonal survival rates of urban deer and then model the impacts different urban deer management strategies have on population growth rates using demographic data from the deer herd in Bloomington, Minnesota, USA.

Study area

I conducted my study in northwest Bloomington (2,971 ha), Minnesota, located approximately 10 km south of Minneapolis, Minnesota. More than 60% of the study area consisted of residential or commercial properties. Greenspace areas, such as parks and conservation areas, comprised about 30% of the study area. Woodlands found in both residential areas and greenspaces were dominated by red oak (*Quercus borealis*), bur oak (*Q. macrocarpa*), and basswood (*Tilia americana*). The 30-year average winter temperature recorded at the Minneapolis International Airport was -8.9° C, with about 126 cm of snowfall (October to May). However, the 1996 to 1997 winter was colder than normal (-9.7° C) with more than normal snowfall for the season (185 cm). During the 1997 to 1998 and 1998 to 1999 winters, however, the average temperature was -5.6° C, and the snowfall was 136 cm.

Methods

Capture and telemetery

From September 5 through January 19, 1998, I captured and radiocollared 34 female deer (7 fawns, 10 yearlings, and 17 adults) using Clover traps (Clover 1956) and a Pneu Dart gun (Pneu Dart Inc., Williamsport, Pa., USA) loaded with succinylcholine chloride (5.6 mg/100 kg body weight). Each animal was physically restrained, fitted with a radiocollar (Advanced Telemetry Systems, Isanti, Minnesota, USA), and aged according to tooth wear and tooth eruption (Severinghaus 1949).

I located each radiocollared deer >5 times per week from October 1996 to January 1998. Location data were collected about once every 6 weeks from February 1998 to March 1999, then again in January 2000 when the study was terminated. Deer killed by vehicles were typically reported to local authorities or to me, providing me with accurate dates for most deer mortalities. Dead deer were located on foot, and the mortality site was inspected in cases where deer were not reported to local authorities, but the mortality sensors were activated, indicating that the deer had died. Cause-specific mortality and survival rates were estimated with MICROMORT software (Heisey and Fuller 1985).

Demographic estimates

For survival analysis, I assumed that the biological year began on June 1, coinciding with parturition. I stratified the year into 3 intervals coinciding with critical life history events (Nixon et al. 1991): summer (June 1 to September 30), fall (October 1 to December 31), and winter (January 1 to May 31). The summer season began at parturition and continued through the weaning period. The fall season coincided with the breeding season. Winter coincided with deer yarding in Minnesota and mortality rates related to the winter severity, and then spring dispersal. Fawns (6 to 12 months old) advanced to the adult age class when they turned 1-year-old.

My data on fawn summer survival rates were limited because fawns with radiocollared females were difficult to observe at parturition and in early summer. I conducted a literature review and assumed fawn summer survival rates for my deer herd were similar to those reported in other studies. I assumed that the minimum value of fawn summer survival was 0.66 (Nelson and Mech 1986) and that the maximum value was 0.90 (Nixon et al. 1991). Values between these extremes would reflect fawn summer survival rates reported by other studies (McGinness and Downing 1977, Bryan 1980, Shultz 1982, Huegal et al. 1985, Nelson and Woolf 1987). I assumed seasonal survival rates for fawns were similar to those of adults after weaning occurred.

I estimated productivity rates for my deer herd using fetus survey data collected for the Twin Cities metropolitan area by the Minnesota Department of Natural Resources (MNDNR) from 1992 to 1998. Wildlife managers and biologists performed necropsies on car-killed female deer during spring to develop annual estimates of productivity. For my modeling efforts, I calculated 95% confidence intervals from these data and assumed a 50:50 sex ratio at birth.

Population model

My purpose for modeling was to evaluate how population growth rates were affected by various management strategies. I avoided using conventional models that require population size and age distribution estimates as an initial parameter in the modeling process because these parameters are difficult to determine and may have substantial impact on the model output. Instead, I used the Leslie matrix model (Leslie 1945, 1948) to evaluate the projection of population growth.

I used a 2×2 matrix model because the fetus survey data collected by the Minnesota Department of Natural Resources were partitioned into fawns and adults. Elements within the model consisted of fawn fecundity (FF), adult fecundity (FA), annual fawn survival (SF), and annual adult survival (SA). I assumed males had little impact on population growth rates; therefore, this model considered

Table 1. Seasonal survival and productivity rates associated with urban deer management strategies under low winter survival conditions. Ranges of values for seasonal survival rates reflect ranges observed for adult radiocollared deer in Bloomington, Minnesota, 1996–1999. Productivity rates reflect the 95% confidence intervals associated with fetus survey data for the Twin Cities metropolitan deer herd, 1992–1998.

Management strategy[2]	Survival rates[1]								Productivity rates	
	Fawn summer	Fawn fall	Fawn management	Fawn winter	Adult summer	Adult fall	Adult management	Adult winter	Fawn	Adult
A	0.66–0.90	0.84–1.00	1.00	0.72	0.93–0.95	0.84–1.00	1.00	0.72	0.22–0.34	1.52–1.76
B	0.66–0.90	0.84–1.00	0.95	0.72	0.93–0.95	0.84–1.00	0.90	0.72	0.22–0.34	1.52–1.76
C	0.66–0.90	0.84–1.00	0.90	0.72	0.93–0.95	0.84–1.00	0.80	0.72	0.22–0.34	1.52–1.76
D	0.66–0.90	0.84–1.00	0.80	0.72	0.93–0.95	0.84–1.00	0.70	0.72	0.22–0.34	1.52–1.76
E	0.66–0.90	0.84–1.00	0.70	0.72	0.93–0.95	0.84–1.00	0.60	0.72	0.22–0.34	1.52–1.76
F	0.66–0.90	0.84–1.00	0.70	0.72	0.93–0.95	0.84–1.00	0.50	0.72	0.22–0.34	1.52–1.76
G	0.66–0.90	0.84–1.00	1.00	0.72	0.93–0.95	0.84–1.00	1.00	0.72	0.22–0.34	1.22–1.41
H	0.66–0.90	0.84–1.00	1.00	0.72	0.93–0.95	0.84–1.00	1.00	0.72	0.22–0.34	1.01–1.17
I	0.66–0.90	0.84–1.00	1.00	0.72	0.93–0.95	0.84–1.00	1.00	0.72	0.22–0.34	0.76–0.88
J	0.66–0.90	0.84–1.00	1.00	0.72	0.93–0.95	0.84–1.00	1.00	0.72	0.22–0.34	0.00
K	0.66–0.90	0.84–1.00	1.00	0.72	0.93–0.95	0.84–1.00	1.00	0.72	0.00	0.00

[1]Survival rates: low and high values for fawn summer survival were based on other studies; low and high values for fawn and adult fall survival rates were based on minimum and maximum adult fall survival rates found in Table 3; fawn and adult management survival rates represent the survival rate associated with the deer management program; fawn and adult winter survival are the low survival rates associated with the severe winter of 1997; adult summer survival rates are the minimum and maximum survival rates found in Table 3.

[2]Management strategy: **A** = no management; **B** = removing 5% of fawn females and 10% of adult females; **C** = removing 10% of fawn females and 20% of adult females; **D** = removing 20% of fawn females and 30% of adult females; **E** = removing 30% of the fawn females and 40% of the adult females; F = removing 30% of fawn females and 50% of adult females; **G** = administering contraceptives to 20% of adult females; **H** = administering contraceptives to 33% of adult females; I = administering contraceptives to 50% of adult females; J = administering contraceptives to 100% of adult females; K = administering contraceptives to 100% of fawn and adult females.

only the female segment of the population. Vital statistics (Tables 1 and 2) were randomly selected based on a uniform distribution within a range of values, then parameterized into the matrix model. Minimum and maximum values represented the lowest and highest survival rates observed during each season across years and the 95% confidence intervals of productivity for each age class. Vital statistics associated with management and winter survival were held constant instead of being randomly determined (Tables 1 and 2). Two model simulations were performed for each management strategy, the first with low winter survival (0.72) and the second with high winter survival (0.94). I ignored emigration because my radiocollared deer exhibited a high degree of fidelity with their seasonal home ranges (Grund et al. 2002), and I also assumed that no immigration occurred.

I generated 1,000 simulations of the model for each management strategy, each simulation represented a random combination of vital rates chosen within the specified bounds, and the dominant eigenvalue (λ) was calculated based on these rates. Populations declined when $\lambda < 1$ and increased when $\lambda > 1$. I calculated a mean λ based on the 1,000 replicates of each model scenario.

Simulations of management strategies

I modeled 11 different management strategies (Tables 1 and 2), each of which was modeled under a low winter survival rate (Table 1) and a high winter survival rate (Table 2). Strategy A illustrated population growth, assuming that no management was in place. Strategies B through F were models projecting light to extensive management programs effectively removing varying fractions of each age cohort using lethal management techniques.

I chose 5 nonlethal management strategies to illustrate how λ was affected by various immunocontraceptive management strategies. For the first 4 models (management strategies G to J), I decreased the adult productivity rate 20 to 100%, assuming that administering contraceptives to these proportions of the female deer herd would effectively reduce the productivity rate in a linear fashion. I also modeled the population assuming all fawn and adult females would receive contraceptives in strategy K.

Results

Demographic estimates

Seventeen of 20 (85%) mortalities were known to be caused by vehicles. Two killed deer were not reported to the local authorities, but their mortality locations were within 50 m of roads. Broken legs and hemorrhaged muscle tissue indicated that death was caused by a vehicle. One deer was killed during a deer removal program conducted by an adjacent community on December 22, 1997. I censored this deer from survival analysis because I was interested in obtaining survival rates of deer that were not killed by wildlife management activities.

With the exception of the severe winter of 1997, seasonal survival rates for adults were high, ranging from 0.84 to 1.00 (Table 3). Similarly, survival among fawns was relatively low during the winter of 1997 (Table 3). The average productivity rate for fawn females was 0.28 fetuses per fawn doe (95% CI = 0.22 to 0.34), and the average productivity for adult females was 1.65 fetuses per adult doe (95% CI = 1.52 to 1.76).

Population model

Results from the 1,000 model simulations under no management program showed marked differences between population growth under low and high winter survival conditions (Table 4, Scenario A). The mean λ was <1 under low winter survival conditions, indicating that the population was decreasing even without a management program in place. In contrast, the population increased by 21% when winter survival was high and no management program was implemented (Table 4, Scenario A).

Model simulations that suggested removing 5 and 10% of fawns and adults, respectively, were insufficient to decrease population growth rates when winter survival was high (Table 4, Scenario B). Population stability was achieved by removing 10% of fawns and 20% of adults (Table 4, Scenario C). However, removing the same percentages of females decreased population growth by 23% under low winter survival conditions (Table 4, Scenario C). When high winter survival rates were modeled, population levels can be decreased by 24% when removing 30 and 40% of the fawns and adults, respectively (Table 4, Scenario E). The population decreased by 33% when low

Table 2. Seasonal survival and productivity rates associated with urban deer management strategies under high winter survival conditions. Ranges of values for seasonal survival rates reflect ranges observed for adult radiocollared deer in Bloomington, Minnesota, 1996–1999. Productivity rates reflect the 95% confidence intervals associated with fetus survey data for the Twin Cities (i.e., Minneapolis-St. Paul, Minnesota) metropolitan deer herd, 1992–1998.

	Survival rates[1]								Productivity rates	
Management strategy[2]	Fawn summer	Fawn fall	Fawn management	Fawn winter	Adult summer	Adult fall	Adult management	Adult winter	Fawn	Adult
A	0.66–0.90	0.84–1.00	1.00	0.94	0.93–0.95	0.84–1.00	1.00	0.94	0.22–0.34	1.52–1.76
B	0.66–0.90	0.84–1.00	0.95	0.94	0.93–0.95	0.84–1.00	0.90	0.94	0.22–0.34	1.52–1.76
C	0.66–0.90	0.84–1.00	0.90	0.94	0.93–0.95	0.84–1.00	0.80	0.94	0.22–0.34	1.52–1.76
D	0.66–0.90	0.84–1.00	0.80	0.94	0.93–0.95	0.84–1.00	0.70	0.94	0.22–0.34	1.52–1.76
E	0.66–0.90	0.84–1.00	0.70	0.94	0.93–0.95	0.84–1.00	0.60	0.94	0.22–0.34	1.52–1.76
F	0.66–0.90	0.84–1.00	0.70	0.94	0.93–0.95	0.84–1.00	0.50	0.94	0.22–0.34	1.52–1.76
G	0.66–0.90	0.84–1.00	1.00	0.94	0.93–0.95	0.84–1.00	1.00	0.94	0.22–0.34	1.22–1.41
H	0.66–0.90	0.84–1.00	1.00	0.94	0.93–0.95	0.84–1.00	1.00	0.94	0.22–0.34	1.01–1.17
I	0.66–0.90	0.84–1.00	1.00	0.94	0.93–0.95	0.84–1.00	1.00	0.94	0.22–0.34	0.76–0.88
J	0.66–0.90	0.84–1.00	1.00	0.94	0.93–0.95	0.84–1.00	1.00	0.94	0.22–0.34	0.00
K	0.66–0.90	0.84–1.00	1.00	0.94	0.93–0.95	0.84–1.00	1.00	0.94	0.00	0.00

[1] Survival rates: low and high values for fawn summer survival were based on other studies; low and high values for fawn and adult fall survival rates were based on minimum and maximum adult fall survival rates found in Table 3; fawn and adult management survival rates represent the survival rate associated with the deer management program; fawn and adult winter survival are the low survival rates associated with the severe winter of 1997; adult summer survival rates are the minimum and maximum survival rates found in Table 3.

[2] Management strategy: **A** = no management; **B** = removing 5% of fawn females and 10% of adult females; **C** = removing 10% of fawn females and 20% of adult females; **D** = removing 20% of fawn females and 30% of adult females; **E** = removing 30% of fawn females and 40% of adult females; **F** = removing 30% of fawn females and 50% of adult females; **G** = administering contraceptives to 20% of adult females; **H** = administering contraceptives to 33% of adult females; I = administering contraceptives to 50% of adult females; J = administering contraceptives to 100% of adult females; K = administering contraceptives to 100% of fawn and adult females.

Table 3. Seasonal survival rates of radiocollared white-tailed deer in Bloomington, Minnesota, 1996–1999.

Age class	Season	Year	*N* deer	Deer days	*N* deaths	Rate	95% CI
Fawn (6–12 mo)	Winter	1997	7	723	2	0.73	0.47–1.00
Adult (>12 mo)	Winter	1997	23	3125	7	0.72	0.56–0.92
		1998	19	2793	1	0.95	0.85–1.00
		1999	16	2385	1	0.94	0.83–1.00
	Summer	1997	20	2358	1	0.95	0.86–1.00
		1998	18	2097	1	0.94	0.84–1.00
		1999	15	1739	1	0.93	0.81–1.00
	Fall	1996	8	728	0	1.00	1.00–1.00
		1997	24	2022	4[1]	0.84	0.70–0.99
		1998	17	1471	1	0.94	0.83–1.00
		1999	14	1274	0	1.00	1.00–1.00

[1] Excludes 1 mortality caused by deer removal program on December 22, 1997.

winter survival rates were modeled and 30% of the fawns and 50% of the adult females were removed from the population (Table 4, Scenario F).

Under high winter survival conditions, populations increased by 15, 10, and 5% when contraceptives were administered to 20, 33, and 50% of the adult females, respectively (Table 4, Strategies G to I). The comparison between λs associated with management strategies A and G illustrates the small effect delivering contraceptives to adult females has on population growth; administering contraceptives to 20% of the adult females decreased λ by only 5%. Under high winter survival conditions, my simulations showed that population levels decreased only when 100% of adult females are treated with contraceptives (Table 4, Scenario J). The comparison between management strategies J and K illustrated how little effect fawn fecundity has on λ; λ did not change when fawn productivity was eliminated.

Discussion

As expected, deer mortalities were caused almost exclusively by vehicles. Studies in northern Minnesota reported high winter mortality rates caused by wolf (*Canis lupus*) predation (Nelson and Mech 1986, Fuller 1990). Studies conducted in Michigan reported losses associated with starvation, particularly among fawns and yearlings (Verme and Ozoga 1971, Van Deelan et al. 1997). Mortalities caused by vehicles probably represented almost all mortalities that occurred in the Bloomington deer herd because few, if any, natural predators coexisted with these deer, food sources were always abundant, and no legal hunting was permitted.

Seasonal survival rates were similar to commonly reported values for deer occupying rural landscapes. As expected, summer survival was high and varied little across the 3 years of study (Nelson and Mech 1986, Fuller 1990, Nixon et al. 1991, Van Deelan et al. 1997). I believe that the high summer survival rates observed with these urban does was a function of reduced home-range size and that these deer were primarily using secluded areas during summer (Grund et al. 2002). As a result, these deer were not crossing roadways and, therefore, were less susceptible to being struck by a vehicle. Fall and winter survival rates were

Table 4. Mean and standard deviations of population growth rates λ associated with various management strategies. Values for survival and reproduction were provided in Tables 2 and 3 then parameterized into a 2×2 matrix model.

Management strategy	Low winter survival (0.72)		High winter survival (0.94)	
	λ^1	SD	λ^2	SD
A	0.93	0.04	1.21	0.06
B	0.85	0.04	1.11	0.05
C	0.77	0.04	1.00	0.05
D	0.67	0.03	0.88	0.04
E	0.58	0.03	0.76	0.04
F	0.51	0.03	0.66	0.03
G	0.88	0.04	1.15	0.05
H	0.85	0.04	1.10	0.05
I	0.80	0.04	1.05	0.05
J	0.62	0.03	0.81	0.04
K	0.62	0.03	0.81	0.04

[1]Management strategy: **A** = no management; **B** = removing 5% of fawn females and 10% of adult females; **C** = removing 10% of fawn females and 20% of adult females; **D** = removing 20% of fawn females and 30% of adult females; **E** = removing 30% of the fawn females and 40% of the adult females; **F** = removing 30% of the fawn females and 50% of the adult females; **G** = administering contraceptives to 20% of adult females; **H** = administering contraceptives to 33% of adult females; **I** = administering contraceptives to 50% of the adult females; **J** =administering contraceptives to 100% of adult females; **K** = administering contraceptives to 100% of fawn and adult females.
[2] Populations decline when $\lambda < 1$ and increase when $\lambda > 1$.

generally high except during winter 1997 when a marked decrease in survival occurred. Deer shifted their home range to residential areas during this severe winter (Grund et al. 2002). As a result, more roads were encompassed within the deer's expanded home ranges during this severe winter; therefore, these deer were more susceptible to being struck by a vehicle.

My model illustrated the increased effectiveness of deer-removal programs over contraception programs. Deer-removal programs are more effective for managing population growth rates in deer because survival contributes more to population growth than fecundity (Nelson and Peek 1982, Grund and Woolf 2004). Similar findings regarding the effectiveness of removal versus contraceptive programs were reported from management models developed for an urban deer herd associated with Irondequoit, New York (Nielsen et al. 1997).

The results from my model regarding contraceptive delivery rates necessary to stabilize and reduce population growth paralleled findings from computer simulations performed by Swihart and DeNicola (1995). Under excellent herd conditions, Swihart and DeNicola (1995) reported that contraceptives would have to inhibit reproduction in 99% of the females for population growth to decrease. Swihart and DeNicola (1995) reported that population growth could be decreased using contraceptives in deer herds with poor growth potential (i.e., herds with lower survival and productivity rates). My model indicated a similar pattern; every contraceptive management strategy decreased population growth under low winter survival conditions. A caveat to managers regarding these observed population growth rates is that the decreased winter survival, which makes the contraceptive program effective, was caused by deer–vehicle collisions.

Contraceptive programs implemented to

manage deer herds can ignore the fawn female segment of the population because growth rates associated with management strategies J and K were identical. Excluding fawns from the management program could substantially decrease the direct costs associated with the program because fawns represent the largest age class in a deer herd and distinguishing between fawns and adults may be possible in the field.

Management implications

Manipulating survival rates in urban deer populations is the wildlife manager's most effective tool in regulating population growth. I recommend removing 20% of adult females from an urban deer population with similar demographic parameters to stabilize population growth and about 40% of the female population to decrease population numbers. Similar to conclusions made by Swihart and DeNicola (1995), I conclude that almost all adult females in a healthy population of deer need to be administered contraceptives for population growth to decrease. Whether delivering contraceptives to this percentage of deer is attainable will probably depend on the population size, age structure of the herd, proper identification of deer, and the amount of effort the municipality is willing to invest in implementing a contraceptive program (Rudolph et al. 2000). I recommend excluding fawns from contraceptive management programs to make the program more cost-efficient.

Deer–vehicle collisions are potentially the most accurate, precise, and easily obtainable life history component for urban deer. In the absence of natural predators, starvation, and hunting, enumerating deer–vehicle collisions will comprise almost all mortalities occurring in an urban deer herd. I recommend that managers construct simple accounting models (McCullough 1984) and incorporate deer–vehicle collisions as a parameter within the model in situations where managers need a population modeling device.

Severe winters may cause deer to move their home range to residential areas (Grund et al. 2002) where they may be more susceptible to deer–vehicle collisions. This suggests that winter mortality rates may fluctuate depending on winter severity, but the primary cause of mortality in urban deer is vehicles, not predation and starvation, as would be expected in rural deer herds (Nelson and Mech 1986, Van Deelan et al. 1997). Managers may consider employing baiting strategies in attempts to reduce seasonal migrations from parks to residential areas.

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