A spatially explicit model of the white-tailed deer population in Delaware

Brian Jennings, Department of Entomology and Wildlife Ecology, University of Delaware, Newark, DE 19716, USA

Jacob L. Bowman, Department of Entomology and Wildlife Ecology, University of Delaware, Newark, DE 19716, USA   *jlbowman@udel.edu*

Elizabeth L. Tymkiw, Department of Entomology and Wildlife Ecology, University of Delaware, Newark, DE 19716, USA

Abstract: Population models of white-tailed deer (*Odocoileus virginianus*) are used by many states to predict population levels and aid in making management decisions. Delaware did not have a deer population model, so we developed one and used it to investigate the implications of changes to the harvest. We modeled 7 changes to the harvest regime and compared these changes to the base line of no changes to the harvest regime. We used survival rates, reproductive rates, harvest data, a population estimate, and spotlight counts to construct the model. The model scenario began in February 2006 and ran until August 2014. Without changing the harvest regime, our model predicted the state deer population to decrease 28%. Allowing Sunday hunting during the opening weekend of the main firearm season and adding an additional week to the main firearm season caused the population to decline at a greater rate. Terminating the Severe Deer Damage Program did not impact the predicted population. Closing the October season for hunting antlerless deer and the January shotgun season both caused a 23% increase to the predicted deer population. The deer population was 11% greater with the January closing of the muzzleloader season and 37% greater with both January shotgun and muzzleloader seasons closed. The model showed that the 17 deer management zones in Delaware have very different population levels and harvest rates. To date, the harvest regimes in Delaware have been changed only at the state level, but future changes to harvest regimes should occur at the zone level.

Key words: Delaware, human–wildlife conflicts, management, *Odocoileus virginianus*, population model, white-tailed deer

Modeling is the process of representing a population through mathematical equations. Models give insight into how animal populations work, predict future population trends, and help wildlife managers make decisions (Akçakaya 2004). Population modeling is an important tool for wildlife management because models allow managers to test management strategies quickly and easily without conducting field experiments (McCarthy 2004). The effectiveness of the different management strategies can be assessed using a model, and the strategy that achieves the desired management goals can be implemented. After implementing the scenario, the manager can then analyze the data to determine if the goals were achieved and if any discrepancies occurred with the inputs to the model (McCarthy 2004).

Sezen et al. (2004) modeled the effects of different hunting regimes on a Turkish mouflon (*Ovis gmelinii anatolica*) population to determine the optimal harvest rate with the least negative impact on the species. In another example, Lopez (2004) modeled the effect of different land development scenarios on the Florida Key deer (*Odocoileus virginianus clavium*) population. These types of models are used as management tools to evaluate proposed changes to current management practices.

White-tailed deer (*Odocoileus virginianus*) population models are a commonly used management tool. Models have been used by many states to generate population estimates and predict future populations, but most models are not used for specific management scenarios before implementation (Xie et al. 1999, Maryland Department of Natural Resources 2009). Maryland and Pennsylvania use models to estimate deer populations, but neither state uses their model to predict future populations when harvest regimes are modified (Maryland Department of Natural Resources 1998, Pennsylvania Game Commission Bureau of Wildlife Management 2002). The models are not used by these states as tools to justify changes in harvest regimes, but as a way of measuring the effect on the population, after harvest regimes have been changed.

Missouri uses a model that simulates the population sizes for each county based on the

number of deer mortalities. The Missouri model was used when implementing restrictions on hunting antlered deer (hereafter, antlerless deer) in parts of the state to determine the required mortality rates to achieve management goals (L.P. Hansen, Missouri Department of Conservation, personal communication). However, the Missouri model is not based on a population estimate, and the model cannot predict the number of harvested deer required to reduce or manage a population at a desired level.

The Delaware Division of Fish and Wildlife (hereafter, Delaware Fish and Wildlife) does not have a white-tailed deer population model to aid in making management decisions. For example, wildlife managers in Delaware were required by policy to add a handgun season to the 2005–2006 white-tailed deer hunting season. Wildlife managers had no way to determine what effect, if any, the new season would have on the deer population. Using a model, the managers could have determined the appropriate season length and bag limit to meet their management goals. A model can provide scientific predictions for managers to justify any changes of harvest regimes. Our objectives were to develop a spatially explicit population model of the white-tailed deer population in Delaware and then to use that model to determine the effect of several changes to the harvest regimes on the white-tailed deer population in Delaware.

Study area

We developed our model for the state of Delaware (total area = 5193.35 km²). Located in the mid-Atlantic region of the United States, Delaware is bordered by Pennsylvania to the north, Maryland to the west and south, and the Delaware River, Delaware Bay, and Atlantic Ocean to the east.

In Delaware, from 1971 to 2000, the average annual high and low temperature in January was 5.6° C and -5.1° C, respectively, and the average annual high and low temperature in July was 26.7° C and 22.8° C, respectively; the average annual precipitation was 113.9 cm (National Oceanic and Atmospheric Administration 2008).
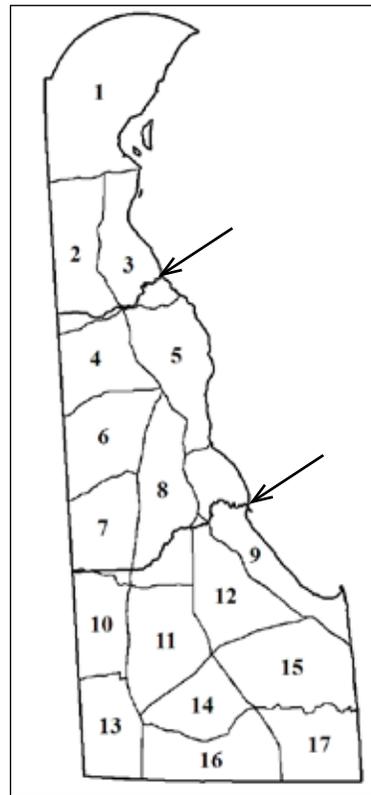
Delaware has 3 counties and 17 deer

Figure 1. Outline map of the state of Delaware and the location of the 17 deer management zones used to model the white-tailed deer population, 2005 to 2014. The county boundaries are shown by the bold lines (arrows).

management zones (Figure 1). The topography north of the Chesapeake and Delaware Canal, which is the southern boundary of Zone 1, is composed of rolling hills. Most of the landscape north of the Chesapeake and Delaware Canal was developed with the cities of Wilmington, Newark, New Castle, and the surrounding suburbs. South of the Chesapeake and Delaware Canal, the topography is flat, and the landscape was dominated by agricultural fields and small woodlots. The primary agricultural crops of Delaware were chickens (*Gallus domesticus*), corn (*Zea mays*), soybeans (*Glycine max*), and wheat (*Triticum aestivum*). Two large urban and suburban areas occurred south of the Chesapeake and Delaware Canal: Dover and the beach resorts of Rehoboth, Dewey, and Bethany. Most (77%) of Delaware was considered deer habitat (Jennings 2009). We defined deer habitat as agricultural, rangeland, forest, and wetlands.

The white-tailed deer (Figure 2) hunting

Figure 2. White-tailed deer (*Odocoileus virginianus*) run from danger. *(Photo by Brett Billings, courtesy U.S. Fish and Wildlife Service)*

seasons in Delaware occurred September 1 to January 31 from 2005 to 2007. The archery season began September 1 and ended January 31. Delaware had 2 muzzleloader seasons; the first one began on the second Friday in October and lasted 9 days until the following Saturday, excluding Sunday. The second muzzleloader season began on the second to last Saturday in January and lasted 8 days until the following Saturday, excluding Sunday. The handgun season in Delaware began on the first Saturday in January and lasted 8 days until the following Saturday, excluding Sunday (Delaware Division of Fish and Wildlife 2007). Delaware had 4 shotgun seasons; the first one was 7 antlerless deer harvest days in October and consisted of the first Friday and Saturday, second to last Monday, Friday and Saturday, and the last Monday and Friday. The main shotgun season began the second Friday in November and lasted 9 days until the following Saturday, excluding Sunday. The third shotgun season was for antlerless deer harvest only, beginning the second Saturday in December and lasting 8 days until the following Saturday, excluding Sunday. The last shotgun season began on the third Saturday in January and lasted 8 days until the following Saturday, excluding Sunday (Delaware Division of Fish and Wildlife 2007).

With the purchase of a license, hunters were permitted to harvest 2 does and 2 antlerless deer. Additional antlerless tags were available for purchase in unlimited quantities. Two additional tags were available for purchase if a hunter wanted to harvest a buck. The hunters-choice tag allowed the hunter to harvest any deer (buck or doe). The quality buck tag allowed the hunter to harvest a buck with an inside antler spread of 38.1 cm or more (Delaware Division of Fish and Wildlife 2007).

Methods

We used the modeling program RAMAS Metapop (Setauket, N.Y.; Akçakaya and Root 2002) to construct a spatially explicit population model of white-tailed deer in Delaware. We used the model to test changes to the current harvest regime on the trajectory of the population. We considered 8 scenarios:

1. No change to the current harvest regime;
2. Permitting Sunday hunting during the opening weekend of the November firearm season;
3. Adding 1 week to the November shotgun season;
4. Termination of the severe deer damage permits;
5. Closing the October antlerless shotgun season;
6. Closing the shotgun season in January;
7. Closing the muzzleloader season in January; and
8. Closing both shotgun and muzzleloader seasons in January.

We modeled each management zone as its own population, and, therefore, investigated the implications of changes to the harvest regime at the scale of deer harvest management for the state. The model began in February 2006 after the conclusion of the 2005–2006 hunting season. We ran each scenario until August 2014.

Stage matrix

We developed an age-structured, sex-specific model of the 17 deer management zones. We modeled fecundity and survival rates for both sexes. We included 2 age classes—fawns (0 to 1 year) and adults (>1 year)—because the Delaware harvest data were provided in these 2 age classes, and the fecundity rates differed between the 2 age classes (fawn: 0.05

[SD 0.03], and adult: 0.94 [0.02]). One form of variability was incorporated using the standard deviation matrix to account for different reproductive success rates and different reported survival rates (Jennings 2009).

Survival

The survival rates used for the stage matrix came from the mean survival rates that we calculated from studies on cause-specific mortality of white-tailed deer (fawn, 0.89 [SD 0.02]; doe, 0.96 [SD 0.02]; buck, 0.95 [SD 0.02]; Jennings 2009). The survival rates we calculated did not include mortality as a result of legal hunting, mortality from hunt-related wounds, poaching, or vehicle collisions. We modeled deer mortality by legal hunting, hunt-related wounds, and poaching, separately. We used the Auto Insurance Industry estimate of 0.06 annual deer mortality in Delaware for deer mortality resulting from automobile collisions (M. Miles, State Farm Insurance, unpublished data, 2008.) The annual deer mortality from the auto industry estimate was similar to the mean vehicle mortalities reported in the literature (Jennings 2009). We subtracted 0.06 from the mean survival rates that we calculated from the literature to account for annual vehicle mortality in the model.

The survival rates in the stage matrix included mortality from natural and unknown causes, disease, drowning, starvation, collisions with trains, and predation by dogs. We did not include mortality from coyote (*Canis latrans*) predation. Delaware lacks a coyote population large enough to affect white-tailed deer survival rates; over the 3-year period from 2006 to 2008, Delaware had only 5 confirmed coyote sightings (J. Rogerson, Delaware Fish and Wildlife, personal communication). Gray wolf (*Canis lupis*) and American black bear (*Ursus americanus*) predation were excluded because Delaware lacks these species.

Fecundity

We calculated the fecundity values using data collected from female deer harvested by hunters and sharpshooters in Delaware, January to April 2006. The deer were taken to a central check station where Delaware Fish and Wildlife staff and volunteers gathered data from the female deer. The does were weighed,

jaws were removed for aging, and the fetuses or ovaries were removed for examination. Does were aged using tooth replacement and wear (Severinghaus 1949). The fetuses were sexed and aged according to Hamilton et al. (1985) with a white-tailed deer fetus scale (Forestry Supply Inc., Jackson, Miss.). If no fetuses were present, the ovaries were removed and examined for corpora lutea of pregnancy or ovulation (Parker and Matson 1995). The mean number of fawns per doe was 0.10 (SD 0.06) and 1.88 (SD 0.04) for the fawn doe and adult doe age classes, respectively.

For both age classes, we divided the number of fawns per doe by 2, which gave the number of male and female fawns at birth. The fetus sex ratio from the deer harvested by sharpshooters and hunters in Delaware was 102:97, male to female (i.e., 1:1 ratio). The number of fawns per doe was used as the fecundity values in the stage matrix.

Population density

The initial zone populations for the model came from a population estimate conducted by Vision Air Research Inc. (hereafter, Vision Air), on December 6 to 17, 2005. Delaware Fish and Wildlife contracted Vision Air to conduct a deer population survey using forward-looking infrared (FLIR). One sample plot, 3.2 km × 12.9 km, was selected within each of the 17 management zones. The sample plots were representative of the percentage of each land cover type in their respective zone based on the 2002 land-use land-cover data.

Vision Air used a Cessna 206 with a FLIR (PolyTech Kelvin 350 II) attached to the left wing and flew transects 152.4 m apart within the 17 sample plots (Bernatas 2006). The number of deer groups and the number of deer in each group were counted in each sample plot. The number of deer observed within the sample plot was divided by the amount of deer habitat in the sample plot, yielding the deer density within the sample plot. The sample plot density was multiplied by the total amount of deer habitat in the zone, yielding an estimate of the deer per zone.

Population demographics

The FLIR survey provided an estimate of the deer density for each zone, but it did not

provide an estimate of the percentages of bucks, does, and fawns in the population; we used spotlight surveys to estimate these percentages. We conducted 5 replications of each spotlight count route before fawns stopped following does, making identification between the two difficult. We drove a survey route in zones 1, 5, and 6. We selected these zones to represent the range of values from rural to more urbanized areas.

Our goal was to see ≤50 identifiable deer along the survey route within each of the 3 zones. Zones 5 and 6 were in rural areas dominated by agriculture, so we conducted the surveys from state, county, and local roads, avoiding roads near zone borders. Zone 1 was dominated by commercial and residential development; therefore, we did not use the state, county, and local roads for the surveys, due to the high traffic volume. Instead, we used Middle Run, a New Castle County park for the Zone 1 survey and drove on park roads and fields for the route.

The surveys began a half hour after sunset and ended before 2400 hours. Only 1 survey route was driven per night due to the length of time required to complete each route. We repeated each survey 5 times, September 5 to October 2, 2007. We drove until we saw ≤50 identifiable deer during the night of the first survey in each zone. We drove the same route during the next 4 replications. We recorded the number of deer clusters, number of bucks, does, or fawns within each cluster, whether the deer were standing or lying, the distance from the vehicle (in meters), and the kilometer along the route where the cluster occurred.

We totaled the number of bucks, does, fawns, and unidentifiable deer for each survey. We divided the number of bucks, does, or fawns by the number of identifiable deer, which gave the percentage of bucks, does, and fawns per route. We calculated the mean percentage of bucks, does, and fawns for the 3 zones. We used the mean percentage of bucks (19%), does (41%), and fawns (40%) to distribute the FLIR population estimates for each zone (Jennings 2009).

Harvest

Harvest data in Delaware were collected using physical check stations and an automated system via telephone or Internet. For the 2005–2006 harvest season, 60% of the deer were checked at physical check stations and 40% were checked using the automated systems. When a hunter reported his or her harvest, a harvest number was assigned to the record. Hunter name, address, phone number, hunting license number and type, hide tag number, zone and county where the deer was harvested, season and weapon used, public or private land, public land code (if applicable), date of harvest, type of tag used, check station code, type of deer killed (i.e., antlered buck, adult doe, button buck, fawn doe, or spike buck), and additional comments were collected for each harvest record. We used the harvest data to estimate the hunting mortalities in each zone.

The harvest data collected from the check stations and the automated system represent the deer legally harvested and recovered. The harvest data did not contain mortalities from poaching or deer fatalities from hunting related wounding. We used survival and mortality studies on white-tailed deer that reported mortality rates for poaching and fatalities from hunting related wounding. We determined that the annual poaching and fatalities from hunting related wounding were 29% of the reported legal harvest (Jennings 2009). We corrected the Delaware-reported harvest data for poaching and fatalities from hunting related wounding by multiplying the reported harvest by 1.29.

We used the average of the 2005–2006 and 2006–2007 Delaware harvest data to estimate harvest rates for our model. Only the 2005–2006 and 2006–2007 harvest data were used because previous years did not provide specific information on the age of the deer and what weapon was used to harvest them. We determined the annual harvest rate for each zone and age class by dividing the mean of the Delaware 2005–2006 and 2006–2007 harvest data by the 2005 FLIR population survey. We calculated the 17-zone mean harvest rates for the 4 stages (adult doe, adult buck, fawn doe, fawn buck). We used the mean annual harvest rates for the 4 stages to predict the future harvest and changes to the deer population.

Scenarios

We manipulated the hunting season in Delaware 7 different ways, based on suggestions from Delaware Fish and Wildlife managers.

Two manipulations involved adding extra days to the November shotgun season. In the other 5 scenarios, we closed different seasons. We also ran a scenario without changing the harvest regimes to compare the effect of the 7 harvest-regime-change scenarios with no change. The harvest season manipulations began in the 2009–2010 hunting season and ran through the 2013–2014 harvest season, a period of 5 years. We ran 1,000 replications of the 8 scenarios for 5 years to predict the population in August 2014. We evaluated the scenarios by looking at the change in the zone populations from the 2005 FLIR population estimate and the change in the statewide deer harvest. We did not evaluate harvest on a zone by zone basis, because we used the 17 zone mean harvest rate as an input and to date managers have only changed harvest regimes at the state level and not at the zone level.

Permitting Sunday hunting during the opening weekend of the November firearm season. Delaware does not allow Sunday hunting due to tradition and social taboos. However, 43 states allow some form of Sunday hunting, because it gives hunters another day to hunt and may lead to increased harvest rates (National Rifle Association Institute for Legislative Action 2009). We modeled the addition of Sunday hunting on private lands during the first weekend of the November shotgun season to evaluate its impact on the overall harvest. We used harvest data from Maryland to model Sunday hunting during the opening weekend of Delaware's November shotgun season.

In 2003 Maryland opened Sunday hunting on private lands, during the opening weekend of the main firearms season, which began on the first Saturday after Thanksgiving and lasted 15 days on the second Sunday, without Sunday hunting. Sunday hunting was allowed only in some of the counties on the eastern shore, central, and western parts of the state. We used the harvest data from Caroline, Cecil, Dorchester, Kent, Queen Anne's, and Talbot counties in Maryland, because they allowed Sunday hunting and were located on the eastern shore, which has similar topography and land use to Delaware. We used the main firearm season harvest data from the previously mentioned counties 4 years before (1999 to

2002) and after (2003 to 2006) Sunday hunting was allowed in Maryland. We compared the 4-year means of the main firearm season harvest before and after Sunday hunting was allowed, to determine the percentage increase in the Maryland main firearm season from Sunday hunting. The addition of Sunday hunting during the first weekend of the main firearm season in Maryland caused a 4% increase in the main firearm season harvest. Therefore, we increased the November shotgun season harvest by 4% to model the addition of Sunday hunting during the opening weekend in Delaware.

Adding 1 week to the November shotgun season. The main shotgun season in Delaware accounted for 46% of all the white-tailed deer harvested during the 2005–2006 hunting season. The October muzzleloader season had the second highest harvest in the 2005–2006 season and accounted for only 12% of the total harvest. The main shotgun season in Delaware lasts only 9 days, without Sunday hunting. Because the main shotgun season accounted for most of the deer harvested in Delaware and it lasted only 9 days, we wanted to see if adding a second week (6 days, Monday through Saturday) would increase the overall deer harvest.

We used the Maryland harvest data from Caroline, Cecil, Dorchester, Kent, Queen Anne's, and Talbot counties because the main firearm season in Maryland lasted 2 weeks and the counties were located on the eastern shore with similar topography and land use to Delaware. We calculated the proportion of deer harvested during the second week of the main firearm season in Maryland by dividing the number of deer harvested in the second week by the total number of deer harvested during the main firearm season. We calculated the mean proportion of deer harvested during the second week of the Maryland firearm season for 8 seasons (1999 to 2006). We determined that the second week of the main firearm season in Maryland accounted for 22% of the total main firearm season harvest. We increased the Delaware November shotgun season harvest by 22% to model the addition of a second week to the November shotgun season in Delaware.

Termination of the severe deer damage permits. In response to increased complaints from farmers about deer damaging agriculture
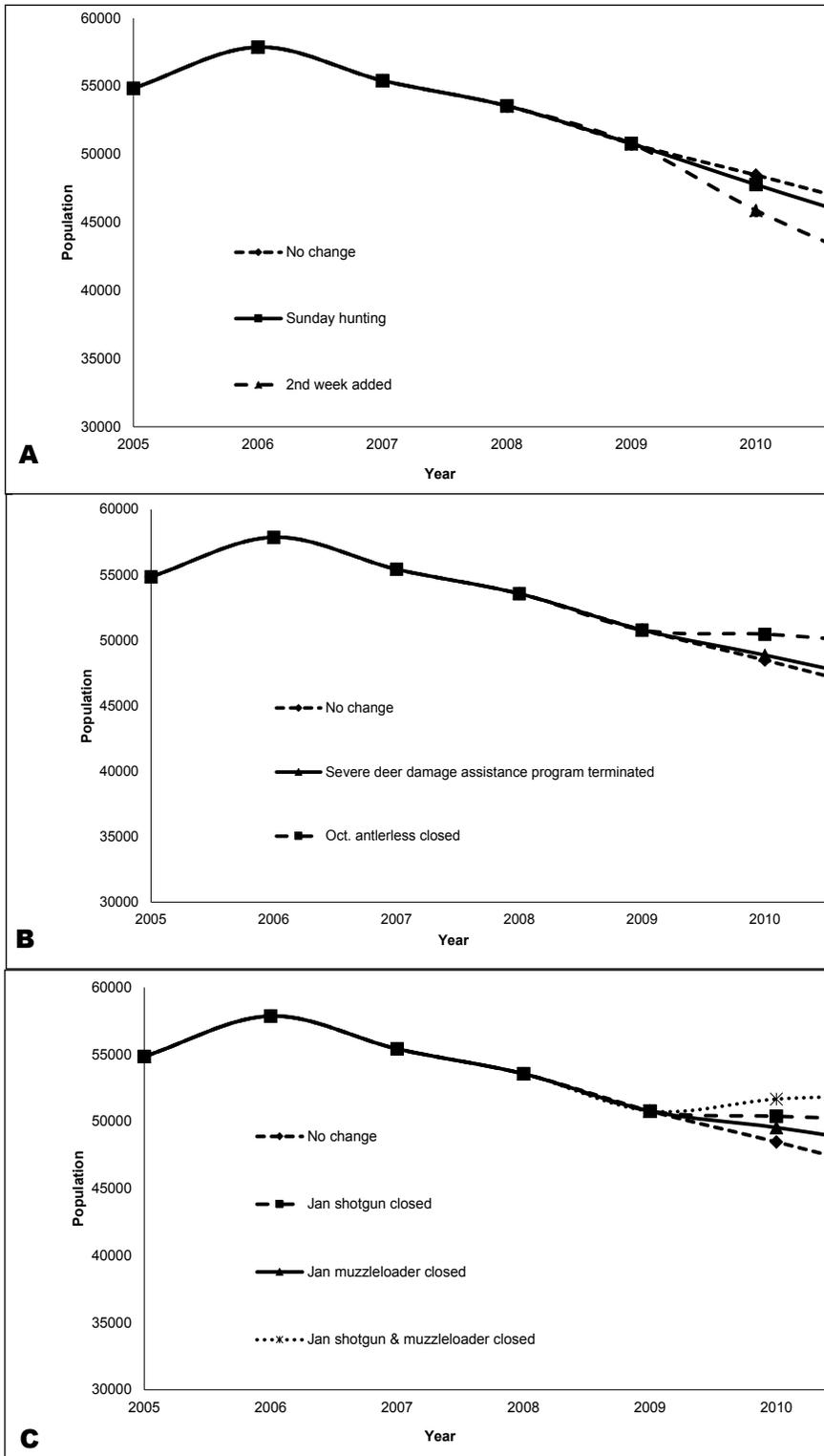
Figure 3. The state of Delaware's white-tailed deer population estimate from the spatially explicit model of the white-tailed deer population beginning August 2005 and ending August 2014. (**A**) The addition of Sunday hunting and 1 week to the November shotgun season compared to no change in the harvest regime. (**B**) The termination of the Severe Deer-Damage Assistance Program and October hunting season for antlerless deer compared to no change in the harvest regime. (**C**) Closing of the January shotgun and muzzleloader seasons compared to no change in the harvest regime.

crops, Delaware Fish and Wildlife managers initiated the Deer Damage Assistance Program in 1996. Farmers enrolled in the program were given free antlerless tags to harvest deer within the hunting seasons (J. E. Rogerson, Delaware Fish and Wildlife, personal communication). In 2005, complaints from farmers about deer damaging agriculture crops caused managers to initiate the Severe Deer Damage Assistance Program, which allowed farmers already enrolled in the Deer Damage Assistance Program for ≤1 year to harvest antlerless deer between August 15 and May 15 (J. E. Rogerson, Delaware Fish and Wildlife, personal communication).

We modeled the termination of the severe deer damage permits to determine if the Severe Deer Damage Assistance Program was effective in reducing the deer population in Delaware. We removed the deer harvested under the severe deer damage permits from the 2005–2006 and 2006–2007 hunting seasons. We took the mean of the 2 hunting seasons with the severe deer-damage permits removed and divided it by the 2005 population estimate. The result was the annual harvest rate for each zone and age class without the deer harvested under severe deer-damage permits. We used the annual harvest rate without the deer harvested with severe deer-damage permits to predict the future harvest and changes in the deer population.

Closing the October antlerless shotgun season. Delaware Fish and Wildlife managers created the October antlerless shotgun season in 2005 to help reduce the deer population. We modeled the closing of the October antlerless shotgun season to evaluate its success in reducing the population. We removed the deer harvested during the October antlerless shotgun season from the 2005–2006 and 2006–2007 hunting seasons. We took the mean of these 2 hunting seasons with the October antlerless shotgun season removed and divided it by the 2005 population estimate. The result was the annual harvest rate for each zone and age class without the deer harvested during October antlerless shotgun season. We used the annual harvest rate without the October antlerless shotgun season to predict the future harvest and changes in the deer population.

Closing the shotgun season in January, closing the muzzleloader season in January, ***and closing both the shotgun and muzzleloader seasons in January.*** The last 3 scenarios we modeled were closing of the January shotgun season, closing of the January muzzleloader season, and closing both shotgun and muzzleloader seasons in January. We modeled these 3 scenarios because Delaware biologists were interested in removing the January muzzleloader and shotgun seasons, or both, to reduce conflicts on public hunting lands among deer hunters and other user groups. Removing one or both of the late January deer seasons could also reduce the number of shed bucks harvested as antlerless deer.

We modeled the closing of the January shotgun season by removing the deer harvested during the January shotgun season from the 2005–2006 and 2006–2007 hunting seasons. We took the mean of the 2 hunting seasons with the deer harvested during the January shotgun season removed, and divided it by the 2005 population estimate. The result was the annual harvest rate for each zone and age class without the deer harvested during the January shotgun season. We used the annual harvest rate without the January shotgun season to predict the future harvest and changes in the deer population. We used the same method to model the closing of the January muzzleloader season and the closing of both shotgun and muzzleloader seasons in January.

Results

Calibration

We calibrated the model by adjusting the harvest and survival rates. We reduced the harvest rate by 15% for the 4 stages in all 8 scenarios. We reduced the survival rates in the stage matrix by 0.07 for the 4 stages. After the reductions, the predicted 2006–2007 harvest was 3% less than the actual harvest and the 2007-2008 predicted harvest was 3% greater than the actual harvest.

Scenarios

Without changing the current harvest regime, the state deer population decreased by 28% to 39,463 (SE 68) deer by the fall of 2014 (Figure 3). All zone populations decreased by year 2014 without modifying the harvest regimes (Table 1). The scenario without changing the harvest regimes was used as a baseline to compare the

Table 1. The predicted percentage population change for the 17 white-tailed deer management zones in Delaware from 2005 to 2014 for the 8 scenarios from a spatially explicit model of the white-tailed deer population in Delaware, 2005 to 2014.

Zone	No change (%)	Sunday hunting added (%)	1 week added to November shotgun season (%)	Severe deer-damage permits terminated (%)	October antlerless season closed (%)	January shotgun season closed (%)	January muzzleloader season closed (%)	January shotgun and muzzleloader seasons closed (%)
1	-11	-15	-28	-8	9	10	-1	22
2	-19	-23	-34	-15	0	1	-9	11
3	-21	-25	-35	-17	-2	-2	-13	8
4	-21	-27	-37	-18	-5	-5	-13	7
5	-29	-32	-41	-25	-12	-13	-20	-3
6	-76	-78	-81	-75	-71	-71	-74	-68
7	-37	-40	-48	-33	-22	-22	-29	-14
8	-31	-34	-43	-27	-15	-14	-23	-5
9	-25	-29	-39	-22	-8	-9	-17	1
10	-48	-51	-58	-46	-37	-37	-43	-30
11	-33	-37	-46	-31	-18	-18	-26	-9
12	-44	-46	-54	-41	-31	-31	-38	-23
13	-71	-72	-76	-70	-65	-65	-68	-61
14	-22	-25	-37	-17	-4	-3	-12	7
15	-16	-19	-31	-12	4	-4	-6	15
16	-24	-28	-38	-20	-6	-6	-16	4
17	-49	-51	-58	-46	-37	-37	-43	-30
Total	-28	-32	-41	-25	-12	-12	-20	-2

effects of changing the harvest regimes in the other 7 scenarios.

The addition of Sunday hunting during the opening weekend of the main firearm season in Delaware caused a 3% increase in the mean harvest rate for the 4 stages (Table 2). The deer population decreased 32% from the 2005 population estimate with the addition of Sunday hunting (Figure 3). By 2014, all zone populations decreased from the initial abundances in 2005 with Sunday hunting (Table 1). Adding a second week onto the November shotgun season increased the mean harvest rate by 11% (Table 2). With the addition of a second week to the November shotgun season, the deer population decreased 41% from years 2005 to 2014 (Figure 3). All of the zone populations decreased by 28% or more by 2014 (Table 1).

We found none of the harvest rates decreased in any of the 4 stages by >0.8% when we removed the deer harvested under the severe-deer-damage permits (Table 2). Terminating

the severe-deer-damage permits still caused the state deer population to decrease by 25% in 2014, and all zone populations decreased, as well (Table 1).

Closing the October antlerless season caused a 6% decrease to the mean harvest rate (Table 2). The decrease to the harvest rate, particularly the adult doe harvest rate, caused the predicted 2014 population in 5 of the zones to increase (Table 1). Despite the increases to some of the zone deer populations, the state deer population declined 12% from 2005 (Figure 3).

Closing the January shotgun season, January muzzleloader season, or both seasons caused the predicted 2014 population to increase in all 3 scenarios (Figure 3). With the January shotgun season closed, the mean harvest rate decreased by 7% (Table 2). Four zone populations increased, 2 zone populations remained the same, and the state deer population declined 12% from 2005 to 2014 (Table 1). Closing the January muzzleloader season caused the state

Table 2. The difference in the predicted 2014 population and the mean harvest rate between the no-change scenario and the 7 scenarios with modified harvest regimes from a spatially explicit model of the white-tailed deer population in Delaware, 2005 to 2014.

Scenario	Change in population	Change in population (%)	Change in mean harvest rate[1]	Change in harvest rate from no-change scenario (%)
No change	0	0	0.0000	0
Permitting Sunday hunting during the opening weekend of the November firearm season	-2,007	-5	0.0091	3
Adding 1 week to the November shotgun season	-7,321	-19	0.0370	11
Termination of the severe-deer-damage permits	1,752	4	-0.0040	-1
Closing the October antlerless shotgun season	9,073	23	-0.0201	-6
Closing the shotgun season in January	9,079	23	-0.0226	-7
Closing the muzzleloader season in January	4,435	11	-0.0107	-3
Closing both the shotgun and muzzleloader seasons in January	14,418	37	-0.0333	-10

[1]The average harvest rate (proportion of the population harvested) of the 4 stages of the model: fawn does, fawn bucks, adult does, and adult bucks.

deer population to decrease 20% by 2014 (Figure 3). All zone populations decreased from years 2005 to 2014, except the zone 1 population, which increased (Table 1). Closing both shotgun and muzzleloader seasons in January had the greatest impact on the predicted 2014 deer population as compared to the no-change scenario—more than any of the 6 other hunting regime changes. Closing both shotgun and muzzleloader seasons in January caused a 10% decrease in harvest rate and 37% increase in the population compared to the no-change scenario (Table 2).

Discussion

The accuracy of a model depends on the quality of the data used to construct the model and the assumptions made by the modeler. The method used to estimate the initial abundances from the FLIR survey could have overestimated or underestimated some of the zone populations and lead to some inaccuracies. The harvest rate used to predict future harvests was fixed, but the actual harvest rate varies each year and would influence the predicted populations.

The model predicted that the deer population was declining under the current harvest regimes. We would expect the harvest rate to decrease because as the population decreases the probability of harvesting a deer should decrease with fewer deer available to harvest. Another problem with the harvest rate was correcting it for poached deer and deer fatalities from wounds related to hunting.

Initial population abundances

We assumed that the 2005 population estimate was an accurate one of the white-tailed deer population; however, the accuracy of the 2005 population estimate is questionable. The population estimates of Zones 6 and 13 were likely underestimated because the number of deer harvested in 2005–2006 and 2006–2007 were greater than the estimated population. FLIR surveys are the most accurate technique for a population census (Belant and Seamans 2000); however, FLIR is not 100% effective, because vegetation blocks the infrared beams preventing the detection of deer in dense vegetation (Belant and Seamans 2000). The

reported detection rates for the Delaware FLIR survey were 100% for agriculture fields and meadows, 86% for deciduous forests, and 50 to 80% for conifer forest, depending on the canopy closure (Bernatas 2006). Bernatas (2006) or the Delaware Fish and Wildlife managers did not adjust the survey numbers for variation in detection rates. Some zone populations likely were underestimated, because deer were not detected during the FLIR survey.

Harvest rate

One of the limitations of using a fixed harvest rate is the number of deer harvested is dependent on the population size. Therefore, as the model population increases, the predicted harvest increases, or, as the model population decreases, the predicted harvest decreases. Steadman et al. (2004) and Bhandari et al. (2006) found factors other than deer population size, such as the number of hunters, weather, number of days spent hunting, distance from roads, and the type of deer harvested, will affect white-tailed deer harvest. We used the average of the 2005–2006 and 2006–2007 harvests to account for the variables identified by Steadman et al. (2004) and Bhandari et al. (2006) that affect the harvest rate other than population size. Despite correcting the harvest rate for yearly variations related to hunter effort, the harvest rate is fixed in the model. We assumed that the harvest rate would remain constant from the 2008–2009 hunting season through the 2013–2014 hunting season. The harvest rate may also increase or decrease based on the deer population size.

We believe that the population estimate was inaccurate in Zones 6 and 13 because the number of deer harvested in 2005–2006 and 2006–2007 were greater than the estimated population of the respective zones. To correct for the inaccuracy of the FLIR population estimate, we used the mean harvest rate for the 17 zones, rather than the individual zone harvest rates. The problem with using the same harvest rate for all the zones was that some zones had very different harvest rates. For example, the mean harvest rate of the 4 stages in Zone 1 was 0.177. The mean harvest rate of the 4 stages in zone 6 zone was 0.691. The 4-stage, mean-harvest rate we used to predict the harvest was 0.322. Because mean harvest

rate was used, the harvest in zone 6 may be underestimated, and the harvests in Zone 1 maybe overestimated. The model predictions in 2014 at the state level maybe accurate within 5% of the actual population and harvest, but the zone level predictions in 2014 may not be accurate within 5%, making it difficult to manage the deer population on a zone level.

The harvest data we received from Delaware Fish and Wildlife represented the deer legally harvested and recovered. The Delaware harvest data did not report poached deer or deer fatalities from wounding related to hunting. We used previous research on cause-specific mortality of white-tailed deer that reported mortality rates for poaching and wounds related to hunting. However, only 6 studies reported poaching mortality, and only 3 studies reported mortality from wounds related to hunting (Jennings 2009). More research is needed to determine if the value we used to correct the Delaware harvest data was accurate.

Problems with RAMAS program

RAMAS was a good modeling program to use, but we encountered 2 problems. RAMAS reproduces the population before harvest occurs and does not let the user choose whether the harvest occurs before or after reproduction within the time step. We would have liked to have the harvest occur before reproduction, because we could have started the model in August 2005 instead of February 2006 and we would not have had to subtract the 2005–2006 harvest from the initial abundance numbers. Because we had to subtract the 2005–2006 harvest from the initial abundance numbers, there was a slight increase in the population from 2006–2007; then it began to decline slowly. The slight increase in the population occurred from not correcting for the inaccuracies of the FLIR population estimate in the 2005–2006 harvest. Because we used the actual 2005–2006 harvest and not the mean harvest rate used to predict the future harvest, the population increased.

The second problem we encountered was that RAMAS reported only the combined harvest for the 17 zones and did not report the individual zone harvests unless each zone was modeled by itself. If RAMAS reported the individual zone

harvest, we could have calibrated the model to the zone level harvest not the state level harvest, making the model predictions more accurate.

No change scenario

Without changing the hunting regimes, the Delaware white-tailed deer population increased in 2006, then began to decline slowly. This prediction may be accurate because hunter and landowner surveys indicate that throughout the state people are not seeing as many deer as in the past (J.E. Rogerson, Delaware Fish and Wildlife, personal communication). The declining population is a reasonable estimate assuming the harvest rates remain constant during the decline.

We believe that some of the zones with more urban development will have increasing rather than decreasing deer populations by 2014. In rural areas dominated by agriculture, hunting is the greatest source of mortality for white-tailed deer populations (Fuller 1990, Brinkman et al. 2004, Bowman et al. 2007). Changing the harvest regimes can be an effective population management tool because managers can control the number of deer harvested by changing bag limits and season lengths. Development is steadily increasing in the areas surrounding the cities of Wilmington, Newark, Dover, and Rehoboth. As development increases in the rural areas, factors like safety zones surrounding buildings will reduce hunting access and create deer refuges (Brown et al. 2000, Bowman 2012). Deer refuges pose problems for wildlife managers using hunting as a management tool to control deer populations because the deer population can grow rapidly within the refuge, overpopulating it and the surrounding areas (Nixon et al. 1991, Brown et al. 2000).

Permitting Sunday hunting during the opening weekend of the November firearm season. The Maryland data showed that adding 1 day during the opening weekend of the main white-tailed deer firearm hunting season can increase the harvest. The success rate for harvesting a deer increases with the number of days spent hunting (Bhandari et al. 2006). An additional harvest day, especially a Sunday when most hunters do not have to work, will give most hunters another day to hunt. The additional day is important to help increase the harvest for hunters who harvest multiple deer.

In Delaware, 60% of the hunters harvest 1 deer, which accounts for 40% of the total harvest; the other 40% of hunters harvest 2 or more deer and account for 60% of the harvest (J. L. Bowman, University of Delaware, unpublished report).

Adding 1 week to the November shotgun season. With the additional 6 days during the main shotgun season, hunters who harvest ≥1 deer would have increased opportunities and success rates to harvest additional deer, thus, increasing the harvest rate (Bhandari et al. 2006). We modeled the addition of the second week to the November shotgun season as a direct increase to the main firearms season. The main shotgun season in Delaware is 9 days and does not include Sunday hunting. The lack of data from surrounding states makes it difficult to determine the effect an additional week on the main firearm season would have on the later hunting seasons. Hunters may have limited time to hunt or may stop hunting because they harvested enough deer during the second week of the November shotgun season and may not harvest deer during the late seasons in December and January. Due to the lack of data, it is difficult to predict how much of an effect the additional week during the November shotgun season would have on the later deer seasons. This is why we modeled the additional week as a pure increase to the harvest rate.

Termination of the severe deer damage permits

The number of deer harvested under the Severe Deer Damage Assistance Program was not great enough to affect the statewide deer population. The effect of the severe deer damage permits is difficult to assess because our analysis evaluated the Severe Deer Damage Assistance Program at the state level and not an individual property level. The program may work on a farm-by-farm basis to reduce crop damage, but not to reduce zone or state deer population levels.

Because the severe Deer Damage Assistance Program is voluntary, landowners' properties not enrolled in the program may act as refuges that protect deer from harvest outside of the regular hunting season (Nixon et al. 1991, Brown et al. 2000). The deer populations in the refuges may restock the surrounding properties

enrolled in the program through dispersing migrants (Nixon et al. 1991). If the deer refuges are restocking the surrounding properties, then we would not expect to detect a landscape effect when modeling the termination of the severe deer damage permits.

Closing the October antlerless shotgun season

Closing the October antlerless shotgun season caused a decrease in the doe harvest rate sufficiently to increase some zone populations, proving that an antlerless-only harvest is an effective method to increase the doe harvest and reduce a deer population (Nixon et al. 1991). The model data contrast with the opinion of Brown et al. (2000) that hunting is not a reliable method to control deer populations. Zone 1 has the highest deer population in Delaware and is the most developed. The deer population in Zone 1 decreased by 11% from 2005 to 2014 with the October antlerless season open. When the October antlerless season was closed, the deer population in Zone 1 increased by 9% from 2005 to 2014. The October antlerless season is important for increasing the harvest success of hunters more willing to harvest antlerless deer (Bhandari et al. 2006). Delaware Fish and Wildlife managers should evaluate the October antlerless season on a zone by zone basis and only close the season in zones with populations below desired levels.

Closing the shotgun season in January, closing the muzzleloader season in January, or closing both

Delaware Fish and Wildlife managers can reduce conflicts between other user groups and deer hunters on public lands by closing the January shotgun or muzzleloader seasons and adding additional firearm harvest days earlier in the season to maintain the current population trend. Delaware Fish and Wildlife managers could close the January shotgun season, add 6 days onto the November shotgun season, and allow Sunday hunting to maintain the current harvest levels and population predictions. If managers made these changes, the population trend would essentially be the same because closing the January shotgun season increased the population by 16% and adding 6 days to the shotgun season and allowing Sunday

hunting resulted in a combined 17% decrease to the 2014 population. Managers could close the January muzzleloader season, as well, but they will need to add additional harvest days on to other seasons like the December antlerless season. Bhandari et al. (2006) found successful hunters of antlerless deer spent a greater number of days afield during the early and late seasons. Closing the January muzzleloader season caused the adult doe harvest mortality to decrease by 1.8%, almost 1% higher than the harvest mortalities of the other 3 stages. If Delaware Fish and Wildlife managers are concerned with decreasing the deer population and reducing conflicts on public lands, then they should close only the late January shotgun or muzzleloader seasons if additional harvest days are added elsewhere.

Management implications

Our model demonstrated that without modifying the harvest regimes the white-tailed deer population in Delaware will decline by 28% in 2014. The model also showed that different zones had different population levels and harvest rates. Currently, changes in harvest regime are implemented statewide, but to better manage the Delaware deer population, managers should set harvest seasons and limits on a zone basis.

If managers choose to manipulate the hunting seasons, several options are available, depending on the desired population level. Managers can further reduce the deer population by allowing Sunday hunting during the opening weekend of the main firearm season or adding an additional week onto the main shotgun season. If managers decide to slow or stop the population decline, then closing the October antlerless season or the late January seasons are the best methods. Terminating the Severe Deer Damage Assistance Program is not an effective method to slow or stop the declining trend. Depending on the desired future population level, managers can adjust the harvest regimes accordingly to meet their population goals.

Acknowledgments

Hansen, Missouri Department of Conservation, and C. Rosenberry, Pennsylvania Game Commission for giving us most of the data required to construct the model and answering our many questions. We thank W. Dunning, G. Schultz, G. Colligan, and M. DiBona for assisting with spotlight counts. Funding for this project was provided by the University of Delaware.

Literature cited

Akçakaya, H. R. 2004. Using models for species conservation and management. Pages 3–16 *in* H. R. Akçakaya, M. A. Burgman, O. Kindvall, C. C. Wood, P. Sjögren-Gulve, J. S. Hatfield, and M. A. McCarthy, editors. Species conservation and management. Oxford University Press, New York, New York, USA.

Akçakaya, H. R., and W. Root. 2002. RAMAS Metapop: viability analysis for stage-structured metapopulations (version 4.0). Applied Bio-mathematics, Setauket, New York, USA.

Belant, J. L., and T. W. Seamans. 2000. Comparison of 3 devices to observe white-tailed deer at night. Wildlife Society Bulletin 28:154–158.

Bernatas, S. 2006. Aerial infrared deer survey for Delaware Division of Fish and Wildlife. Vision Air Research Inc., Boise, Idaho, USA.

Bhandari, P., R. C. Steadman, A. E. Luloff, J. C. Finley, and D. R. Diefenbach. 2006. Effort versus motivation: factors affecting antlered and antlerless deer harvest success in Pennsylvania. Human Dimensions of Wildlife 11:423–436.

Bowman, J. L. 2012. The role, size, and effectiveness of safety zones for creating refuges for white-tailed deer. Human–Wildlife Interactions 6:291–297.

Bowman, J. L., H. A. Jacobson, D. S. Coggin, J. R. Heffelfinger, and B. D. Leopold. 2007. Survival and cause-specific mortality of adult male white-tailed deer managed under the quality deer management paradigm. Proceedings of the Annual Conference of the Southeast Association of Fish and Wildlife Agencies 61:76–81.

Brinkman T. J., J. A. Jenks, C. S. DePerno, B. S. Haroldson, and R. G. Osborn. 2004. Survival of white-tailed deer in an intensively farmed region of Minnesota. Wildlife Society Bulletin 32:726–731.

Brown T. L., D. J. Decker, S. J. Riley, J. W. Enck, T. B. Lauber, P. D. Curtis, and G. F. Mattfeld. 2000. The future of hunting as a mechanism to control white-tailed deer populations. Wildlife Society Bulletin 28:797–807.

Delaware Division of Fish and Wildlife. 2007. 2007/'08 Delaware hunting seasons, <http://www.fw.delaware.gov/Hunting/Pages/Hunting-Seasons.aspx>. Accessed March 31, 2008.

Fuller, T. K. 1990. Dynamics of a declining white-tailed deer population in north-central Minnesota. Wildlife Monographs 110:1–37.

Hamilton, R. J., M. L. Tobin, and W. G. Moore. 1985. Aging fetal white-tailed deer. Proceedings of the Annual Conference of the Southeast Association of Fish and Wildlife Agencies 39:389–395.

Jennings, B. 2009. A spatially explicit model of the white-tailed deer population in Delaware. Thesis, University of Delaware, Newark, Delaware, USA.

Lopez, R. R. 2004. Florida Key deer (*Odocoileus virginianus clavium*) effects of urban development and road mortality. Pages 450–458 *in* H. R. Akçakaya, M. A. Burgman, O. Kindvall, C. C. Wood, P. Sjögren-Gulve, J. S. Hatfield, and M. A. McCarthy, editors. Species conservation and management. Oxford University Press, New York, New York, USA.

Maryland Department of Natural Resources. 1998. "Charting the course for deer management in Maryland" a management plan for white-tailed deer in Maryland, <http://www.dnr.state.md.us/wildlife/dmp.html> Accessed May 31, 2006.

Maryland Department of Natural Resources. 2009. Maryland white-tailed deer plan: 2009–2018, <http://www.dnr.state.md.us/irc/docs/00014598.pdf>. Accessed August 19, 2014.

McCarthy, M. A. 2004. Mammal population viability modeling. Pages 433–437 *in* H. R. Akçakaya, M. A. Burgman, O. Kindvall, C. C. Wood, P. Sjögren-Gulve, J. S. Hatfield, and M. A. McCarthy, editors. Species conservation and management. Oxford University Press, New York, New York, USA.

National Oceanic and Atmospheric Administration. 2008. Climatography of the United States No. 81. Monthly station normals of temperature, precipitation, and heating and cooling degree days 1971–2000, <http://hurricane.ncdc.noaa.gov/climatenormals/clim81/DEnorm.pdf>. Accessed August 19, 2014.

National Rifle Association Institute for Legislative Action. 2009. The truth about Sunday hunting:

why hunters shouldn`t be treated as second-class citizens, <http://www.nraila.org/issues/factsheets/read.aspx?id=174&issue=021>. Accessed March 6, 2009.

Nixon, C. M., L. P. Hansen, P. A. Brewer, and J. E. Chelsvig. 1991. Ecology of white-tailed deer in an intensively farmed region of Illinois. Wildlife Monographs 118:1–77.

Parker, L. H., and G. M. Matson. 1995. Laboratory analysis of North American deer ovaries: techniques and interpretation. Post paper. The Wildlife Society Second Annual Conference. Portland, Oregon, USA.

Pennsylvania Game Commission Bureau of Wildlife Management. 2002. Draft: management plan for white-tailed deer in Pennsylvania (2003–2007), <http://www.wpconline.org/daily-photos/pa_game_commission_deer_mgt.pdf>. Accessed August 19, 2014.

Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195–216.

Sezen, Z., H. R. Akçakaya, and C. C. Bilgin. 2004. Turkish mouflon (*Ovis gemelinii anatolica*) in central Anatolia. Pages 459–468 *in* H. R. Akçakaya, M. A. Burgman, O. Kindvall, C. C. Wood, P. Sjögren-Gulve J. S. Hatfield, and M. A. McCarthy, editors. Species conservation and management. Oxford University Press, New York, New York, USA.

Steadman, R., D. R. Diefanbach, C. B. Swope, J. C. Finley, A. E. Luloff, H. C. Zinn, G. J. San Julian, and G. A. Wang. 2004. Integrating wildlife and human-dimensions research methods to study hunters. Journal of Wildlife Management 68:762–773

Xie, J., H. R. Hill, S. R. Winterstein, H. Campa III, R. V. Doepker, T. R. Van Deelen, and J. Liu. 1999. White-tailed deer management options model (DeerMOM): design, quantification, and application. Ecological Modelling 124:121–130.

BRIAN JENNINGS (photos of authors unavailable) is a fish and wildlife biologist with the U.S. Fish and Wildlife Service (USFWS) at the Chesapeake Bay Field Office in the Partners for Fish and Wildlife Program. He received his B.S. degree in wildlife conservation with a minor in coaching from the University of Delaware (UD) in 2005 and his M.S. degree in wildlife ecology from UD in 2010. Prior to working for the USFWS, he worked for the Delaware Division of Fish and Wildlife in the Landowner Incentive Program. Currently, he works with private landowners to restore fish and wildlife habitat in Delaware and Maryland, with a focus on stream and wetland projects.

JACOB L. BOWMAN is a professor of wildlife ecology and chair of the Department of Entomology and Wildlife Ecology at the University of Delaware. He received his B.S. degree in forestry and wildlife with a minor in biology from Virginia Tech in 1992, his M.S. degree in wildlife ecology with a minor in statistics from Mississippi State University (MSU) in 1996, and his Ph.D. degree in forest resources with an emphasis in wildlife ecology from MSU in 1999. Additionally, he has worked for the U.S. National Park Service at Shenandoah National Park and has contracted with the U.S. Department of Defense at the Armed Forces Experimental Activity. His research interests include human–wildlife interactions, GIS applications in wildlife ecology, population dynamics, and carnivore and large mammal ecology and management.

ELIZABETH L. TYMKIW is a biologist working for the University of Delaware. She received her B.S. degree in environmental science from the University of Maryland–College Park in 2005 and her M.S. degree in wildlife ecology from the University of Delaware in 2010. She has worked as a biologist for the federal government, local conservation organizations, and private consulting companies.