ELSEVIER

Ecological Modelling 124 (1999) 121–130

ECOLOGICAL MODELLING

www.elsevier.com/locate/ecolmodel

White-tailed deer management options model (DeerMOM): design, quantification, and application

Jialong Xie [a,*], Harry R. Hill [b], Scott R. Winterstein [a], Henry Campa III [a], Robert V. Doepker [c], Timothy R. Van Deelen [d], Jianguo Liu [a]

[a] *Department of Fisheries and Wildlife, Michigan State University, 13 Natural Resources Building, East Lansing, MI 48824, USA*

[b] *Michigan Department of Natural Resources, Wildlife Division, Lansing, MI 48909, USA*

[c] *Michigan Department of Natural Resources, Norway, MI 49870, USA*

[d] *Illinois Natural History Survey, Champaign, IL 61820, USA*

Received 19 January 1999; received in revised form 26 May 1999; accepted 15 June 1999

Abstract

The deer management options model (DeerMOM) is a computer simulation model designed to assess the effects of management options on population size, sex and age structure of white-tailed deer (*Odocoileus virginianus*). In this model, we grouped deer into three age classes: fawn, yearling, and adult. Reproductive rates and fetal sex ratios were age-specific, while natural and harvest mortality rates were both age- and sex-specific. DeerMOM was parameterized to represent the deer population in the Upper Peninsula of Michigan, USA. Effects of winter severity were incorporated into the model. Population estimates derived from annual pellet group surveys were used to validate the model. Different management options were evaluated using two criteria: a quantity goal (number of deer) and a quality goal (percentage of antlered bucks in the deer population). Simulation results indicated that current management practices (with a high rate of buck harvest) resulted in high deer numbers with a low percentage of antlered bucks. Under the condition of high buck harvest rate, increasing doe harvest did not achieve both the quantity and the quality goals simultaneously. Moderate harvest of both sexes would control population growth and increase the percentage of antlered bucks. The simulations also showed that winter weather conditions and doe harvest shaped deer population trends but buck harvest determined the percentage of antlered bucks. Our findings indicated that quality deer management objectives can be reached only by lowering buck harvest rates while simultaneously increasing the doe harvest. The best option for achieving both the quantity and the quality goals was moderate harvest of bucks and does without sex bias.

Keywords: DeerMOM; Harvest management; *Odocoileus virginianus*; Population modeling; Quality deer management; White-tailed deer

* Corresponding author. Tel.: +1-517-3535468; fax: +1-517-4321699.
E-mail address: jxie@perm3.fw.msu.edu (J. Xie)

PII: S0304-3800(99)00157-X

1. Introduction

White-tailed deer (*Odocoileus virginianus*) is one of the most important game species in North America. This species provides opportunities for hunting and recreation, but also causes serious socioeconomic and ecological concerns, such as deer-vehicle accidents, crop damage, and impacting forest regeneration (Caughley, 1981; McShea et al., 1997). Given the conflicting interests surrounding deer, it is essential to establish management goals that consider the needs and requirements of different stakeholders as well as the integrity of the ecosystem. Based on the established goals, deer managers can then determine the appropriate measures needed to achieve their specific objectives. Harvesting is a primary option for population manipulation.

Deer management requires instruments that can assess the effects of harvesting options on deer population size and structure. Computer modeling can help wildlife managers understand deer population dynamics and choose a better alternative to reach their objectives (Walters and Gross, 1972; McCullough, 1979; Starfield, 1997). Good models can incorporate essential information and allow evaluation of the consequences of different management options.

There are basically two approaches to modeling deer population dynamics. One approach is to build empirical models such as 'stock-recruitment' models. The stock-recruitment models are constructed through empirical data fitting instead of mechanistic functions (McCullough, 1979). The use of empirical models is limited because they do not describe population sex and age structure, which are important parameters to deer managers. The other approach is to build mechanistic models, such as a density-dependent matrix harvest model (Jensen, 1996) and models based on POP-II (Bartholow, 1986; Bender and Roloff, 1996) and its predecessor ONEPOP (Walters and Gross, 1972; Medin and Anderson, 1979). The matrix model considers age-specific mortality and fecundity, but does not describe sex structure. POP-II and its predecessor track animals through each annual cycle. These 'accounting' models require detailed data, including pre- and post-harvest season natural mortality, harvest and wounding loss, age-specific vulnerability, and age-specific reproductive rates (Bartholow, 1986). Both modeling approaches have their advantages and disadvantages. The empirical models incorporate the expertise of wildlife managers but do not address some underlying mechanisms and do not provide crucial information needed for deer management. On the other hand, the mechanistic models provide more scientific reasoning and explanation but require much more data.

We developed a hybrid (mechanistic and empirical) model, the deer management options model (DeerMOM), to evaluate the effects of deer management options on population size, sex and age structure. Mechanisms in DeerMOM are similar to those in POP-II, but DeerMOM also incorporates management empiricism. Our model takes advantage of all the data available from field studies, yet it is not limited by data incompleteness. DeerMOM is designed to simulate deer populations in different locations but was parameterized and tested for the deer population in the Upper Peninsula (UP), Michigan, USA. The objectives of this paper are to introduce the design of the model and the quantification of the model parameters, and to demonstrate its application in deer management under the specific constraints of management goals in the UP of Michigan.

2. Methods

2.1. Model design

We followed three principles to design our model: simplicity, accuracy, and management orientation. These principles were incorporated into the process of model design, construction, validation, and simulation. They are also interconnected and not separable.

2.1.1. Simplicity

The model should be structured as simply as possible. The deer populations in most areas are heavily hunted, which reduce their life expectancy relative to natural deer populations (Burgoyne, 1981). Because of the differences between managed and natural deer populations, we grouped deer into three age classes: fawn (< 12 months), yearling (13–24 months), and adult (> 24 months) to simplify model structure. This classification is widely accepted and adapted by deer managers (McCullough, 1979). We divided mortality into harvest mortality and natural mortality (e.g. vehicle accidents, starvation, predation). We used annual mortality instead of seasonal mortality to ease data collection and model application.

2.1.2. Accuracy

The model should simulate and predict population dynamics as accurately as possible. Knowledge of age and sex composition of deer population is essential for deer managers to establish their management objectives. Since male deer are polygamous, only female deer numbers have a substantial impact on changes of population size. However, the percentage of bucks in the population is of special interest to deer hunters and consequently deer managers. In our model, we simulated the dynamics of males and females separately. We used age- and sex-specific natural mortality and harvest mortality. In addition, we differentiated their reproductive rates and fetal sex ratios by age class for female deer.

2.1.3. Management orientation

The final principle was to develop a model that is management oriented. Management goals could be used as criteria to evaluate harvest strategies under defined time frames. A user could set goals and run the model to determine which harvest scenarios would achieve the management goals during a predefined time period. Specific management goals include maximum sustainable yield, trophy management, and quality deer management. A user could also change the model structure by adding or removing some components, or by modifying parameter values. However, the model should be user friendly and have a graphical user interface to assist users in learning and using the model. In addition, model results should be transferred easily to other software programs for further data analysis. Finally, the model should accommodate users with different levels of expertise in modeling and mathematics.

To fulfil the above-mentioned requirements, we used Stella to develop DeerMOM. Stella is a multi-level, hierarchical environment for constructing models (High Performance Systems, 1997) which allows DeerMOM to have a three-level hierarchical structure. The first level is a user interface, where novice users can change parameter values by using sliders or numerical pads. Moreover, the user can inspect simulation results using tables and graphs as well as export them to other programs through dynamic data exchange. At the second level, a more advanced user can access the model structure in order to modify the structure and manipulate parameter values. Finally, an expert user can access the third level to review the mathematical equations and to learn the model mechanisms in detail.

2.2. Model structure

DeerMOM consists of five interconnected sectors: female, male, birth/death, harvest and population (Fig. 1). DeerMOM operates on an annual cycle that starts on 1 October and ends on 30 September of the following year.

2.2.1. Female sector

Females were grouped into three age classes: fawn, yearling, and adult as mentioned previously. For each annual cycle, surviving newborn females enter the female fawn group, and similarly surviving fawns recruit to the female yearling

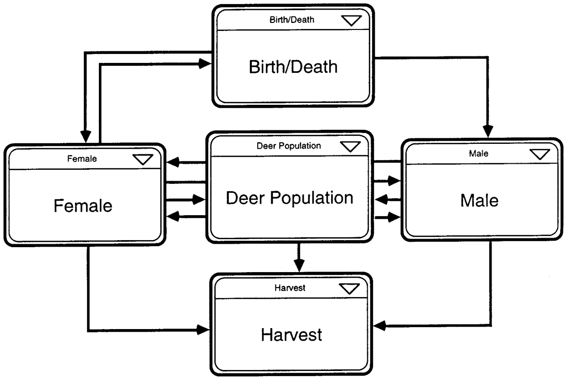


Fig. 1. Part of the user interface in DeerMOM showing the five sectors.

group, surviving yearlings to the female adult group. Adult females that survive the hunting season and natural mortality remain in the adult age class. Natural mortality for each age class was density- and harvest-dependent and influenced by winter severity.

2.2.2. Male sector

The male sector had the same model structure as the female sector, but parameter values were quantified differently. For example, the harvest rate for male adults was different from that for female adults. As with females, all mortality rates were age- and sex-specific.

2.2.3. Birth/death sector

Changes in the deer population size and structure depend on the dynamics of both births and deaths. We assumed that immigration and emigration would not affect age and sex structure of the population. Thus, any addition to the population comes from the offspring of female fawns, yearlings, and adults. To estimate newborn females and males, we used female number in spring, reproductive rate, and sex ratio for each age class. The spring female number in each age class was estimated by subtracting harvest and natural mortality from the previous fall female number in each age class. Deaths were a result of harvest mortality and natural mortality. Mortality rates were age- and sex-specific.

2.2.4. Harvest sector

We included all harvest-related information in this sector. Specifically the sector contained age and sex composition of harvest, total harvest, percentage of antlered bucks and antlerless deer in the harvest.

2.2.5. Population sector

We included population initialization, management goals, and all data related to age and sex distribution of deer in this sector. The population was initialized by size, sex ratio, and percentage of deer number in each age class. This sector also extended the female and male sectors by deriving population statistics of interest. Specifically, it contained numbers and sex ratios for each age class, numbers of females and males, total population size, sex ratio, density, and percentage of antlered buck in the population.

2.3. Quantification of the model

The most important parameters for DeerMOM included age-specific reproductive rates, fetal sex ratios, neonatal mortality, age- and sex-specific natural mortality, and harvest mortality. DeerMOM was parameterized to represent the deer population in the UP of Michigan, USA. As winter weather conditions greatly influence the population dynamics in the UP, winter severity indices (WSIs), which measured air chill and snow hazard (Verme, 1968), were incorporated into the model. Data for estimating model parameters were obtained from the Michigan Department of Natural Resources (MDNR) and recent field studies (Van Deelen et al., 1997).

2.3.1. Reproductive rates

Reproductive rates were defined as average fetuses per female based on spring surveys (Friedrich and Schmitt, 1988; Verme, 1989). From March to May, the MDNR personnel conducted necropsies of female deer that died from vehicle collisions and other accidents. Female deer were aged and their fetuses were counted if they were pregnant. Based on these data, reproductive rates were calculated for fawns, yearlings, and adults. The MDNR discontinued these surveys in the UP after 1988. In DeerMOM, we used the data from the MDNR spring surveys from 1973 to 1988 because these data provided an adequate sample for analytical purposes. Reproductive rate ranges were 0–0.14, 0.8–1.55, 1.67–2.33 with an average of 0.05 (0.01, S.E.), 1.30 (0.05), and 1.84 (0.05) for female fawns, yearlings, and adults, respectively.

As reproductive rates showed a great annual variability, regression analyses and F-tests were used to detect whether or not the variability was associated with population size. No significant relationship was detected between population and the reproductive rates of yearlings ($F_{1,14} = 0.399$, $P = 0.538$) and of adults ($F_{1,14} = 0.036$, $P = 0.852$) from 1973 to 1988. However, there was a significant decrease for fawn reproductive rates as population size increased ($F_{1,14} = 7.891$, $P = 0.014$). These findings were consistent with the reproductive patterns found in southern Michigan (Verme, 1989). Even so, as fawn deer had very low reproductive rates (0.05) in the UP, changes in fawn reproductive rates had a minimal impact on the entire population.

Regression analyses showed that reproductive rates for fawns were positively associated with reproductive rates for adults ($F_{1,14} = 7.969$, $P = 0.026$), while reproductive rates for yearlings were not associated with reproductive rates for adults ($F_{1,14} = 4.407$, $P = 0.633$). To account for the annual variability of reproductive rates, a uniform random function was used to estimate the reproductive rates for female adults and yearlings. The estimates of reproductive rates for fawns were derived from regression equation $Y = -0.0002X + 0.1269$ ($R^2 = 0.3605$, $F_{1,14} = 7.969$, P $= 0.026$), where Y is the reproductive rate for fawns, and X is the reproductive rate for adults.

2.3.2. Fetal sex ratio

Sex ratio was defined as the percentage of males in each age class. Fetal sex ratio was the percentage of newborn males in offspring. Verme's (1983) data were used to determine fetal sex ratio. The fetal sex ratios for female fawns, yearlings, and adults were 62.5, 52.6 and 50.6%, respectively.

2.3.3. Mortality

Causes of mortality were classified as harvest mortality and natural mortality. The harvest mortality was estimated from MDNR harvest survey data (Verme, 1989). The natural mortality was based on a radio-collared deer study in the UP from 1992–1994, where the deer population was exposed to hunting (Van Deelen et al., 1997). We partitioned the natural mortality into three additive parts: base mortality, winter mortality, and harvest compensatory mortality (HCM). The base mortality was the mortality when the population density was low (< 5 deer/km^2) and winter weather was very mild. Base mortality may be largely due to vehicle accidents or old age. The winter mortality was mainly due to malnutrition during severe winter conditions. Cumulative WSIs, which summed the weekly WSIs from December to April, were used to relate winter severity to deer winter mortality. The cumulative WSIs in the UP ranged from 65.7 in 1987 to 147.7 in 1979, with an average of 105.4 from 1969 to 1996. To estimate winter mortality, we scaled the difference between the actual WSI and the lowest WSI in the UP (65.7) by a different adjustment factor for fawns, yearlings, and adults. HCM was a function of deer density and harvest mortality. Harvest mortality was assumed to be compensatory to density-dependent mortality (DDM). In other words, DDM would be lower under a higher harvest rate. HCM was mainly a result of predation, diseases, vehicle accidents, and other unknown causes.

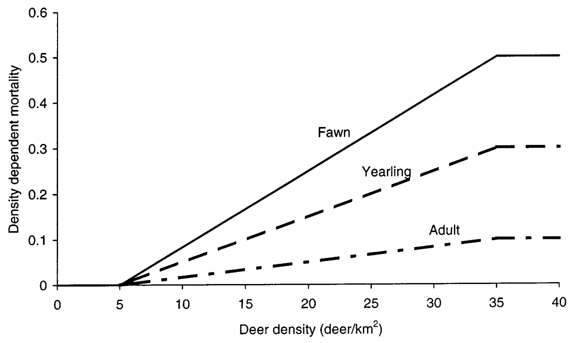


Fig. 2. Relationship between density-dependent mortality and deer density, assuming that there was no deer harvest.

We used a two-step procedure to calculate HCM. The first step was to estimate DDM, assuming that there was no harvest. If deer density was 5 deer/km^2, DDM(age) was assumed to be 0 for all age classes. Five deer/km^2 was used as the minimum density ($D_{\min}$) because DDM(age) could be negligible when deer density was 5 deer/km^2 in the UP. When deer density was between 5 and 35 deer/km^2, it was assumed that there was a linear relationship between DDM(age) for each age class and deer density (Fig. 2). If deer density was 35 deer/km^2, the maximum DDM ($DDM_{\max}$(age)) was assumed to be 0.5, 0.3 and 0.1 for fawns, yearlings and adults, respectively. Thirty-five deer/km^2 was used as the maximum density ($D_{\max}$) for DDM because it could be the carrying capacity in Michigan (McCullough, 1979). In mathematical terms, for a deer population with density D, age-specific DDM can be expressed as Eq. (1):

$$\mathrm{DDM(age)} = \begin{cases} 0 & (\text{if } D \leq 5) \\ (D - D_{\min}) * \mathrm{DDM}_{\max}/(D_{\max} - D_{\min}) & (\text{if } 5 < D < 35) \\ \mathrm{DDM}_{\max}(\mathrm{age}) & (\text{if } D \geq 35) \end{cases} \quad (1)$$

The second step to calculate HCM was to consider the compensatory effect of harvest and to estimate adjusted DDM. Because deer harvest might mitigate DDM, we then adjusted DDM by a factor of (1 − harvest rate(H)) for each respective age class. In mathematical terms, age specific HCM can be expressed as Eq. (2):

$$\mathrm{HCM(age)} = (1 - H(\mathrm{age})) * \mathrm{DDM(age)} \quad (2)$$

Take male yearling as an example. If the deer population density was 15 deer/km^2 and the harvest rate for male yearlings was 50%, then DDM for male yearlings was $(15 - 5)*0.3/(35 - 5) = 0.1$, and the HCM was $0.1*(1 - 0.5) = 0.05$.

To summarize, the calculation of annual natural mortality can be expressed as Eq. (3):

$$\mathrm{NM(age)} = \mathrm{BM(age)} + (\mathrm{WSI} - \mathrm{LWSI})*\mathrm{SF(age)} + \mathrm{HCM(age)} \quad (3)$$

where NM is natural mortality, BM is base mortality, WSI is winter severity index, LWSI is the lowest winter severity index, and SF is a scale factor.

2.3.4. Neonatal mortality

Winter weather has a significant impact on fetal development during late gestation and thus influences natal survival (Verme, 1977). Because of this impact, we partitioned neonatal mortality into two parts: base neonatal mortality and neonatal mortality due to winter severity. Base neonatal mortality was the mortality when winter weather was very mild (low WSI). Based on Verme's (1977) data, we used the following equation to estimate neonatal mortality:

$$\mathrm{NnM} = \mathrm{BNnM} + (\mathrm{WSI} - \mathrm{LWSI})*\mathrm{SF} \quad (4)$$

where NnM is the neonatal mortality, and BNnM is the base neonatal mortality, other variables are defined in previous equations.

2.4. Model initialization

The 1989 fall population in the UP of Michigan was used to initialize DeerMOM. Population size was estimated from pellet group surveys. Sex ratio and age distribution were based on MDNR deer checking station data (Hill and Rabe, 1989).

2.5. Model testing

DeerMOM was run 50 times to simulate deer population from 1989 to 1996 using a 1-year time step. Annual harvest data and WSIs from MDNR were used in these simulations. The 1989–1996 fall population estimates from annual pellet group surveys were used to verify simulation results from DeerMOM. Paired t-tests were used to compare population estimates (1990–1996) from the pellet group surveys and DeerMOM simulations. After the model was verified, the 1996 fall population estimate, harvest data during 1996–1997 hunting season, and WSIs for the winter of 1996–1997 were used to predict the 1997 fall population.

2.6. Simulation scenarios

We ran 50 simulations of 35 representative management scenarios resulting from the combinations of seven buck harvest rates and five doe harvest rates. Buck harvest rates ranged from 10 to 70% with 10% intervals and doe harvest rates ranged from 5 to 25% with 5% intervals. Based on the deer checking station data, the harvest rates for female and male fawns were assumed to be 5%. We simulated deer population dynamics from 1989 to 1996 using actual WSIs. These scenarios were evaluated by whether they could reach the management goals by 1996. The management goals included a quantity goal (372,500 deer in the fall) and a quality goal (35% antlered bucks).

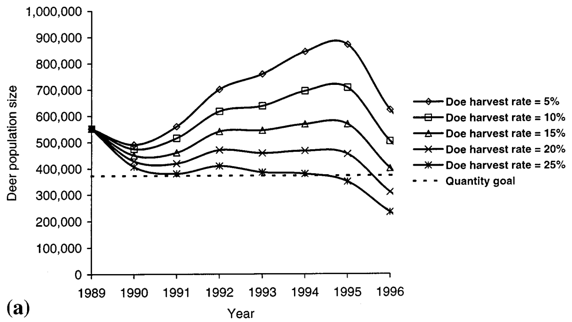
We chose the optimal scenario, defined as the scenario that could most closely achieve both goals by 1996, to project the 1996 deer population for the next 5 years (from 1997 to 2001) under different weather conditions (mild, moderate, harsh and random). WSIs were set at 80, 100 and 120 for mild, moderate, and harsh winters, respectively. WSIs were assumed to be constant for 5 consecutive years, except when WSI was a random function, where the WSIs were uniformly distributed random numbers between 80 and 120.

3. Results

DeerMOM simulated deer population well and there was no significant difference ($t = 1.24$, d.f. $= 6$, $P = 0.26$) between the population estimates from DeerMOM and those from the pellet group surveys (Fig. 3). DeerMOM predicted that the 1997 fall population was 528 307, which is 11.5% higher than the MDNR estimate of 474 000 deer.

When the buck harvest rate was 50%, which was similar to the current buck harvest rate, harvesting more does reduced the population size dramatically (Fig. 4a) but only slightly increased the percentage of antlered buck. Thus, the quality goal was not reached (Fig. 4b).

When doe harvest rates remained constant, decreasing buck harvest rates did not change deer population sizes markedly (Fig. 5a) but increased the percentage of antlered bucks greatly (Fig. 5b). The best scenario in terms of management goals was the harvest of 20% of both bucks and does. It brought the population down to the quantity goal level (Fig. 5a) and increased the percentage of antlered bucks near the quality goal level (Fig. 5b).



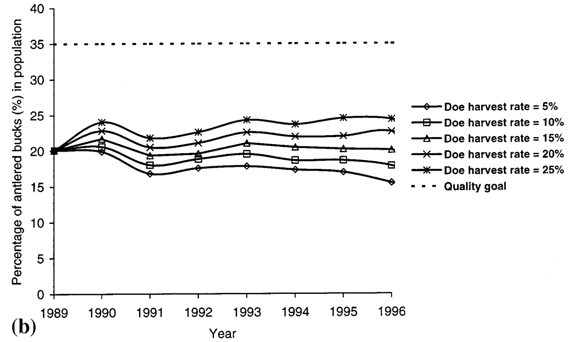


Fig. 4. (a) Population dynamics under different doe harvest rates when 50% of bucks were harvested. (b) Dynamics of percentage of antlered bucks under different doe harvest rates when 50% of bucks were harvested.

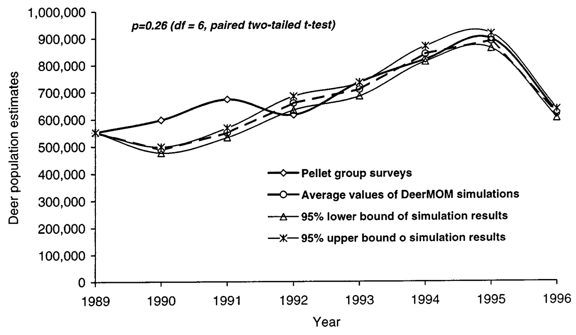


Fig. 3. Comparison between population estimates from DeerMOM simulations and from pellet group surveys.

Winter severity had a dramatic impact on the population. When 20% of bucks and does were harvested, it took 5 years to reach the quantity goal under moderate (WSIs = 100) winters (Fig. 6a). When winter conditions were continuously harsh (WSIs = 120), deer population decreased rapidly. When the winter conditions were mild (WSIs = 80), the population remained stable (Fig. 6a). However, regardless of WSI, the percentage of antlered bucks increased to the goal level (Fig. 6b) if 20% of bucks and does were harvested.

Winter weather conditions were very important in determining appropriate harvest rates for achieving the quantity goal. Under harsh winters, it was necessary to lower the harvest rate from 20 to 5% (Fig. 7a). Under mild winters, however, the harvest rate should be increased from 20 to 30%

(Fig. 7a) to reach the quantity goal. Both harsh and mild winter conditions allowed deer to reach the quality goal level under either 5 or 30% harvest rates if harvest rates were the same for both female and male deer (Fig. 7b).

4. Discussion

4.1. Model structure

In this study, we tried to balance model simplicity, accuracy, and generality in order to be accessible to the wildlife management community (Levins, 1966). We minimized data requirements for the model but still offered vital population information, which is crucial for deer management decision processes. The model structure could be easily modified to include new information once it is available. For example, if there are field data available for neonatal mortality, it is easy to replace the empirical function with actual data.

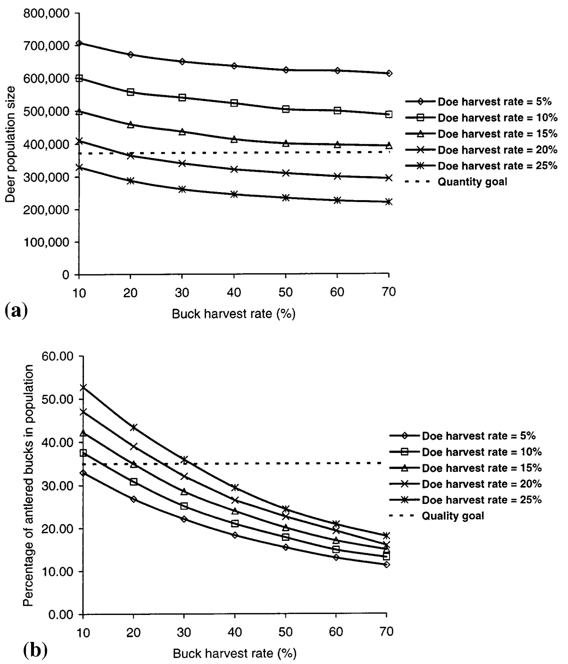


Fig. 5. (a) Population size in 1996 under different management scenarios. (b) Percentage of antlered bucks in 1996 under different management scenarios.

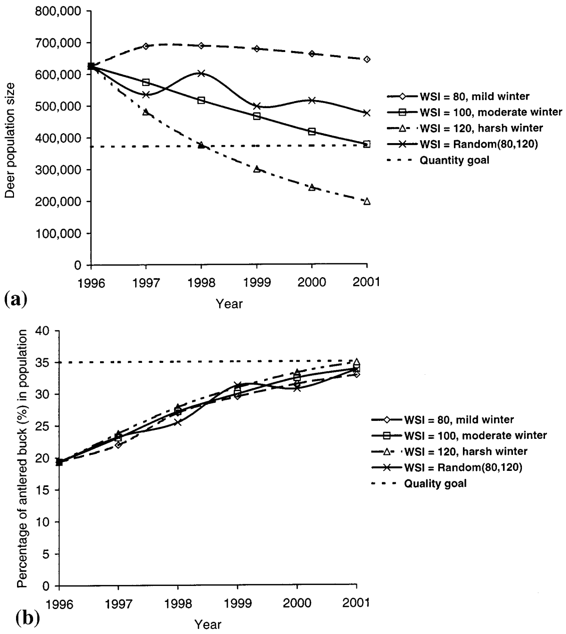


Fig. 6. (a) Effect of winter severity on population dynamics (Buck and doe harvest rates = 20%). (b) Effect of winter severity on dynamics of the percentage of antlered bucks (Buck and doe harvest rates = 20%).

4.2. Quantification of parameters

Quantification of model parameters is usually the most challenging step in systems modeling. We felt comfortable with age-specific reproductive rates because good historical data existed. There is controversy about how maternal age and nutritional conditions affect offspring sex ratios (Harder, 1980; Verme, 1983; Burke and Birch, 1995). Because of this controversy, we used Verme's (1983) data as they were based on research on deer in the UP. However, we did not incorporate yearly variation in fetal sex ratios because the data were not available.

We took an empirical approach to estimate natural mortality and neonatal mortality. Because harsh winter weather accounted for most of deer mortality in winters, winter mortality was linked with WSIs. This approach might oversimplify the relationship between deer mortality and weather conditions, however, simulations suggested these estimates are reasonable.

To apply DeerMOM to other deer populations, model parameter values should be changed to reflect the biological and ecological characteristics of those populations (Euler and Morris, 1984; Gavin et al., 1984; Dusek et al., 1989). The most important changes might be the estimates of natural mortality and neonatal mortality. Winter severity might not play such an important role in regulating deer population in warmer geographical areas as it did in the UP.

4.3. Current management practices

Although the MDNR tended to adapt ad hoc regulations in the UP because of the unpredictability of harsh winters, they realized that more consistent proactive management regulations should and could be implemented in the field. The winters of 1995–1996 and 1996–1997 were harsh and greatly decreased the UP deer population by up to 50%. Nevertheless, the deer population in the UP remains higher than the goal level and the MDNR continues to issue antlerless deer permits to reduce the deer population. There are some local experiments, such as Hiawatha Sportsmans Club's 1996 resolutions, to harvest more antlerless deer and restrain buck harvest (T.R. Minzey, MDNR, Personal communication). However, no such statewide effort has been implemented to discourage the harvest of antlered bucks. Under current management practices, the quality goal can not be reached (Van Deelen et al., 1997).

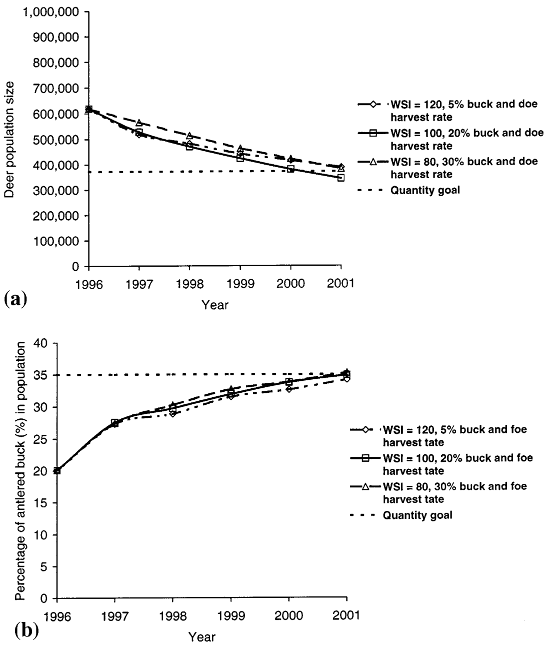


Fig. 7. (a) Deer population dynamics in response to low harvest rates under harsh winters (WSIs = 120) and high harvest rates under mild winters (WSIs = 80). (b) Percentage of antlered bucks in response to low harvest rates under harsh winters (WSIs = 120) and high harvest rates under mild winters (WSIs = 80).

4.4. Harvest recommendations

Our recommendations are mainly based on ecological considerations. Which option is the best to implement in management practices also depends on acceptability of a specific management option by stakeholders. However, the advantages of DeerMOM is that it offers options that a wildlife manager can assess their outcomes before the specific harvest scenario is implemented, thus it offers a logical and defensible rationale for wildlife decision making (Starfield, 1997).

Our recommendation of harvesting 20% of both bucks and does is based on then existing population size, management goals, winter severity conditions, and the time frame previously defined. Accordingly, the 20% harvest rates should not be interpreted as a general guideline to other populations. However, our model reveals that doe harvest is a more effective way to manage population size and buck harvest is a more effective way to manage the percentage of antlered bucks. This finding has important implications in quality deer management. To reach both the quantity and the quality goals, managers must balance both buck and doe harvest rates. Contrary to wildlife manager's intuitive viewpoint that simply increasing doe harvest would increase the percentage of antlered buck to the goal level (McCullough, 1979), our simulations show that the quality goal cannot be reached without also decreasing buck harvest simultaneously. In other words, the quality goal can only be achieved by restricting the buck harvest and increasing the doe harvest.

Acknowledgements

We thank K. Mattson-Hansen, E. Langenau and D. Rabe for their data, suggestions and comments on our model. We appreciated the insights and advice from C. Bennett, L. Leefers, J. Sikarskie and S. Schmitt. We are also grateful to C. Lepczyk and two anonymous reviewers for their comments on our draft. The Wildlife Division of Michigan Department of Natural Resources funded this study through Federal Aid in Wildlife Restoration Act under the Pittman-Robertson Project W-127-R.

References

Bartholow, J., 1986. POP-II system documentation. Fossil Creek Software, Ft. Collins, Colorado, USA.

Bender, L.C., Roloff, G.J., 1996. Modeling deer harvest alternatives in Indiana. Trans. Illinois State Acad. Sci. 89, 63–71.

Burgoyne, G. Jr, 1981. Observations on a heavily exploited deer population. In: Fowler, C.W. (Ed.), Dynamics of Large Mammal Populations. Wiley, New York, pp. 403–413.

Burke, R.L., Birch, J.M., 1995. White-tailed deer vary offspring sex-ratio according to maternal condition and age. Ecol. Res. 10, 351–357.

Caughley, G., 1981. Overpopulation. In: Jewell, P.A., Holt, S. (Eds.), Problems in Management of Locally Abundant Wild Mammals. Academic Press, New York, pp. 7–20.

Dusek, G.L., Mackie, R.J., Herriges, J.D. Jr, Compton, B.B., 1989. Population ecology of white-tailed deer along the lower Yellowstone River. Wildlife Monograph 104, 1–68.

Euler, D., Morris, M., 1984. Simulated population dynamics of white-tailed deer in an any-deer hunting system. Ecol. Model. 24, 281–292.

Friedrich, P.D, S.M. Schmitt, 1988. Doe productivity and physical condition: 1988 Spring survey results. Wildlife Division Report No. 3083. Michigan Department of Natural Resources, Lansing, MI.

Gavin, T.A., Suring, L.H., Vohs, P.A. Jr, Meslow, E.C., 1984. Population characteristics, spatial organization, and natural mortality in the Colombian white-tailed deer. Wildlife Monograph 91, 1–41.

Harder, J.D., 1980. Reproduction of white-tailed deer in the north central United States. In: Hine R.L., Nehl S. (Eds.), White-Tailed Deer Population Management in the North Central States. Proceedings of a Symposium held at the 41st Midwest Fish and Wildlife Conference, Urbana, IL, 10 December, 1979, pp. 23–35.

High Performance Systems, Inc., 1997. STELLA® II Technical Documentation. Hanover, NH.

Hill, H.R., D.L. Rabe, 1989. Deer checking station data — 1989. Wildlife Division Report No. 3126. Michigan Department of Natural Resources, Lansing, MI.

Jensen, A.L., 1996. Density-dependent matrix yield equation for optimal harvest of age-structured wildlife populations. Ecol. Model. 88, 125–132.

Levins, R., 1966. The strategy of model building in population biology. Am. Scientists 54, 421–431.

Medin, D.E., Anderson, A.E., 1979. Modeling the dynamics of a Colorado mule deer population. Wildlife Monograph 68, 1–77.

McCullough, D.R., 1979. The George Reserve deer herd: population ecology of a K-selected species. University of Michigan Press, Ann Arbor, MI.

McShea, W.J., Underwood, H.B., Rappole, J.H. (Eds.) 1997. The Science of Overabundance: Deer Ecology and Population Management. Smithsonian Institution Press, Washington, DC.

Starfield, A.M., 1997. A pragmatic approach to modeling for wildlife management. J. Wildlife Manag. 61, 261–270.

Van Deelen, T.R.H., Campa, I.I.I., Haufler, J.B., Thompson, P.D., 1997. Mortality patterns of white-tailed deer in Michigan's Upper Peninsula. J. Wildlife Manag. 61, 903–910.

Verme, L.J., 1968. An index of winter weather severity for northern deer. J. Wildlife Manag. 32, 566–574.

Verme, L.J., 1977. Assessment of natal mortality in Upper Michigan deer. J. Wildlife Manag. 41, 700–708.

Verme, L.J., 1983. Sex ratio variation in Odocoileu: a critical review. J. Wildlife Manag. 37, 545–552.

Verme, L.J., 1989. Decline in doe fawn fertility in southern Michigan deer. Can. J. Zool. 69, 25–28.

Walters, C.J., Gross, J.E., 1972. Development of big game management plans through simulation modeling. J. Wildlife Manag. 36, 119–128.