

MODELING THE EFFECTS OF NUTRIA (*MYOCASTOR COYPUS*) ON WETLAND LOSS

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Abstract: We created a model to study the process in which nutria (*Myocastor coypus*) feeding activities lead to erosion and loss of marsh area. This model ties together data on nutria population dynamics and feeding behavior from the literature with data from field studies on the phenology of *Scirpus americanus* and *Spartina patens* conducted in the Barataria Basin, Louisiana, USA in 1992. The complete model consists of three linked models: a model of nutria population dynamics (nutria model), a model of the annual marsh biomass cycle of *Scirpus americanus* and *Spartina patens* (biomass model), and a plant-biomass density-dependent marsh area model (area model). When all three models are linked together, they form the "nutria-biomass-area model." Analysis of the models indicated the following. (1) The high population densities and low survivorship rates as reported in the literature are incompatible. (2) The nutria model is sensitive to adult and juvenile survivorship and, to a lesser extent, young born per female. It is not particularly sensitive to gestation periods, impregnation rates, or time to maturity. (3) The marsh area model is not sensitive to the marsh loss equation nor to the density at which loss of marsh area begins but is sensitive to the amount of biomass destroyed per nutria. (4) Nutria numbers do not significantly decrease in the nutria-biomass-area model until the total marsh area approaches zero because marsh loss occurs only during winter when marsh biomass is at its annual low.

Key Words: nutria, *Myocastor coypus*, *Scirpus americanus*, *Spartina patens*, eat-out, brackish marsh, marsh loss, model, population dynamics, coastal Louisiana

INTRODUCTION

Nutria (*Myocastor coypus* Molina) are wetland rodents native to South America, south of 15° latitude. They have been widely introduced to Europe, Japan, and North America (Nowak 1991). Nutria escaped from captivity in southern Louisiana, USA in the late 1930s and 1940s, became established in the Louisiana coastal marshes (Kinler et al. 1987), and by 1950, their population in Louisiana was estimated to be 20 million (Nowak 1991).

In Louisiana, nutria have been associated with the loss of brackish and freshwater marshes because of a process known as "eat out" (Harris and Webert 1962, Foote and Johnson 1993, Linscombe and Kinler 1997). In an eat out, nutria reduce the aboveground biomass by foraging on the basal portion of stems and break up the root mat by grubbing for roots and rhizomes (Ehrlich 1962). During subsequent periods of high water, the substrate may be washed away, leaving a hole in the marsh. As nutria move their feeding activities to nearby areas, the marsh becomes fragmented, more vulnerable to natural erosive forces, and eventually begins to break up.

Although nutria population dynamics, marsh loss, and marsh dynamics have been studied, our review of the literature indicates that there has not been an integration of these separate studies. We developed a model that integrated our studies of the biomass dynamics of *Scirpus americanus* Pers. and *Spartina patens* (Aiton) Muhl. (Johnson and Foote 1997) with what has been reported in the literature about nutria population dynamics. We had three purposes in creating the model. First, we wanted to link data from the literature on nutria population dynamics with our data on marsh plant phenology. A simulation model provides a framework for doing just that. Second, we wanted to identify gaps in our current knowledge as a means of directing future research. Third, we wanted to begin development of a tool, the model, that would be useful in making management decisions in the future.

METHODS

The nutria-biomass-area model consists of three linked models (Figure 1): a nutria population dynamics model (nutria model), a marsh biomass model for

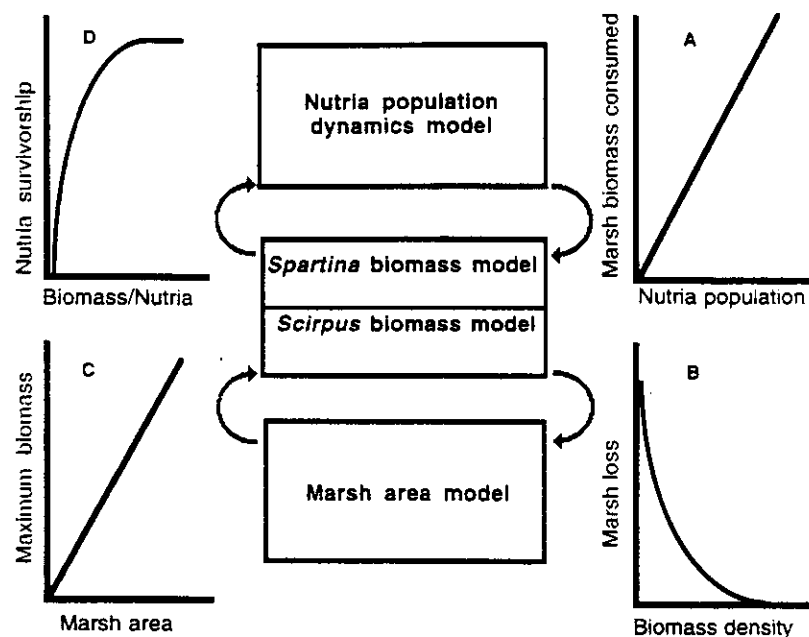


Figure 1. The conceptual model. The model is composed of three linked submodels. The nutria population interacts with the two biomass submodels by removing biomass in proportion to the nutria population (A). The biomass model interacts with the marsh area model through density-dependent marsh loss (B). Loss in marsh area feeds back into the maximum sustainable biomass by reducing total maximum biomass. As area decreases, the total available biomass decreases (C). The reduction in marsh area in turn feeds back to the nutria population model by affecting the amount of biomass available for nutria consumption (D).

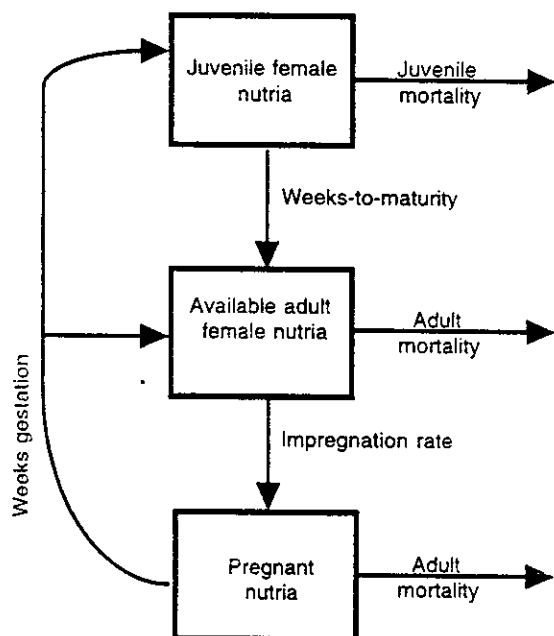


Figure 2. Nutria population dynamics conceptual model. Female nutria were divided into three classes: juveniles, adult available (i.e., not pregnant), and adult pregnant. The two adult classes had the same mortality rates, which differed from the juvenile mortality rates. The mortality rate had two additive components, a fixed "natural" mortality rate and mortality rate that was a function of food availability.

Spartina patens and *Scirpus americanus* (biomass model), and a marsh area loss model (area model). The model is available for downloading and inspection via a web site (Carter et al. 1998). The basic logic of the nutria-biomass-area model is as follows.

(1A) As the number of nutria increases, the amount of biomass consumed increases. As the biomass is consumed, the density of biomass decreases.

(1B) Once biomass decreases below a certain amount, a percentage of marsh area is lost. The lower the density, the greater the rate of loss.

(1C) As the area of marsh decreases, the total amount of biomass that the marsh can support decreases.

(1D) The less biomass, the fewer nutria that can be supported.

The model was created with STELLA[®] (High Performance Systems Inc. 1994), version 3.06, and simulations were performed with both Macintosh and Windows versions. The model time step was 1 week, and the interval between calculations was 0.5 time steps, using the Euler's approximation. To test different hypotheses, we made minor modifications to the basic model.

Nutria Population Model

The nutria model has three stocks: juvenile females, available adult females and gestating adult females

Table 1. Standard parameters used in the nutria-marsh loss model. These are the default parameters used by the model. For the standard simulation, the impregnation rate was a linear function of nutria population density and varied between 12.5% and 100%. Ranges reported are for this study.

Parameter	Standard Value	Range Varied	Source
Annual adult survivorship	30%	10–90%	1, 2
Annual juvenile survivorship	20%	10–90%	2
Young-per-female	6	3–14	3
Gestation period	19 weeks	15–25	3, 4
Time-to-maturity	20 weeks	5–50 weeks	3
Initial juvenile	0	0–10	arbitrary
Initial available females	10	0–40	arbitrary
Initial gestating females	10	0–50	arbitrary
Male:female	1:1	not varied	
Value of juvenile	0.5	not varied	not available
Individual biomass need (kg/nutria/week)	96.25	0–204	1
Density dependent impregnation rate	function of nutria density	12.5–100%	5
Constant impregnation rate	no standard rate	10–100%	not available
Critical vegetation density	1800 kg/ha	0–1800 kg/ha	not available
Minimum vegetation density	200 kg/ha	not varied	not available

(1) Willner 1982; (2) Nowak 1991; (3) Kinler *et al.* 1987; (4) Evans 1970; (5) Reggiani *et al.* 1995.

(Figure 2). In the model, adult females are pregnant for a gestation period, a length of time that is constant within a simulation. At the end of the gestation period, they give birth to juvenile nutria and become available females. The juvenile nutria remain juveniles for a period of time that is constant within a simulation until they become adult available females. Males are modeled implicitly by assuming a 50:50 sex ratio (Kinler *et al.* 1987). The gestation period and time to maturity were held constant for the entire year, even though there is evidence that time to maturity may vary with season or food availability (Linscombe *et al.* 1981, Willner 1982). During sensitivity analysis, key parameters, such as gestation period, survivorship, and time to maturity, were varied to determine their effect on nutria population dynamics (Table 1).

Reggiani *et al.* (1995) reported that the percentage of females pregnant increased with increasing population densities, so we derived a impregnation rate function (Equation 1) from data in their Figures 1 and 2.

Impregnation rate = $0.1902 \times (\text{nutria/ha}) + 0.539$:

Min = 0.125, Max = 1.0

($n = 6$, adjusted $r^2 = 0.6379$, $p = 0.0567$) (1)

Because equation 1 gives percentage of nutria pregnant and not the rate at which females become pregnant, it overestimates pregnancy rate when the percentage of nutria pregnant is small and is fairly close when impregnation rates are high.

Annual juvenile and adult survivorship estimates from the literature (Newson 1969) were transformed into weekly natural mortality rates. The natural mor-

tality rate was held constant for the duration of a simulation. The weekly mortality rate for juveniles and adults was an additive function of both the natural mortality rate and a food-based mortality rate we obtained by using Equation 2.

Weekly Mortality Rate = Natural Mortality Rate +

If: [Available Biomass < Biomass Need]

Then: $[1 - (\text{Available Biomass} \div \text{Biomass Need})]$

Else: 0. (2)

Predation is not accounted for explicitly in this model and is assumed to be a component of the natural mortality rate.

The variable "young-per-female" was held constant for a given simulation. There is evidence that reabsorption of fetuses is an important response to periods of stress in female nutria (Atwood 1950, Newson 1969, Evans 1970). We used equation 3 to model reabsorption of fetuses during food stress.

Fecundity = Young-per-Female*

If: [Available Biomass < Biomass Need]

Then: $[1 - (\text{Available Biomass} \div \text{Biomass Need})]$

Else: 1. (3)

The amount of biomass nutria consumed per week was calculated from daily biomass consumption measurements we found in the literature (Willner 1982). Nutria eat only a small portion of the plant material that they destroy while foraging (Harris and Webert 1962). The ratio of consumed-to-destroyed biomass

has been estimated at ten-to-one (Greg Linscombe, Louisiana Department of Wildlife and Fisheries, personal communication). Therefore, our weekly biomass consumption includes a multiplier of 10 to account for this "waste." For estimating the amount of biomass consumed, we used an equation in which the number of nutria was equal to twice the number of adult females plus the number of juvenile females (Equation 4).

Adult Equivalent Nutria

$$= (1 + \text{sex ratio}) \cdot \text{adult females} \\ + 1/2 \cdot (1 + \text{sex ratio}) \cdot \text{juvenile females}, \quad (4)$$

where the sex ratio is the number of males divided by the number of females per hundred individuals. Therefore, the model assumes that the juveniles eat half of what an adult eats. We used this as an approximation because it was convenient. We have no evidence concerning the amount juvenile nutria eat, and this amount probably changes with age. For these simulations, we assumed the nutria consumed *Scirpus americanus* and *Spartina patens* biomass in equal proportions.

Biomass Model

The biomass model was divided into two biomass submodels: one for *Spartina patens* and one for *Scirpus americanus*. The models were fitted to data on aboveground biomass accumulation and loss in plots protected from nutria grazing (Johnson and Foote 1997). The species-specific growth and loss rates, which were measured over two- to three-month intervals, were converted to weekly rates, and these rates were used to calculate each week's aboveground biomass (Eq. 5.)

$$\text{Biomass}_{(\text{week } i-1)} \\ = \text{Biomass}_{(\text{week } i)} (\text{growth rate}_{(\text{week } i)} + \text{loss rate}_{(\text{week } i)}) \quad (5)$$

These values were then adjusted so that the ungrazed biomass density for each species in the simulation never exceeded the maximum or minimum values measured for that species in the field. There was no grazing-induced compensatory growth in the model.

Marsh Area Model

The marsh area model assumes that loss of marsh area is a function of vegetation biomass density. The "critical density" is the vegetation density at which marsh loss begins. The "minimum density" is the vegetation density at which all marsh area is lost. The simulation started with 20 ha of marsh. The 20-ha size

was based on literature information of nutria movement patterns (Coreil 1976, Willner 1982, Gosling and Baker 1989) and was selected to be the smallest area large enough to contain a deme. When the vegetation density is larger than the critical density, no marsh area is lost. Between the critical and minimum density, the rate of marsh loss was controlled by one of three marsh loss equations: constant (Equation 6), linear (Equation 7), and geometric (Equation 8).

If: Vegetation Density < Minimum Density

Then: Marsh Loss Rate = 1.0

Else If: Vegetation Density > Critical Density

Then: Marsh Loss Rate = 0.

Constant Loss Equation

$$\text{Else: Marsh Loss Rate} = 0.1 \quad (6)$$

Linear Loss Equation

$$\text{Else: Marsh Loss Rate} \\ = -0.000625 \times \text{Vegetation Density} \\ + 1.125 \quad (7)$$

Geometric Loss Equation

$$\text{Else: Marsh Loss Rate} = \text{Minimum Density} \\ \div \text{Vegetation Density} \quad (8)$$

The linear marsh loss equation was the default equation used in these simulations. The marsh area model assumes that all marsh area loss is permanent (Linscombe and Kinler 1997).

To conduct sensitivity analysis and explore model behavior, the model was run in two modes: with all three component models linked together, the nutria-biomass-area model; and with the component models run separately or two at a time. The model was considered sensitive to a parameter if changes in that parameter caused significant changes in model output for variables such as nutria population size or timing and severity of marsh loss. Nutria population sizes for the last 61 weeks of the simulation were analyzed with box-and-whiskers plots. We chose the last 61 weeks because this period covered model dynamics for the last year of the simulation. A parameter change that resulted in a non-overlap of the 10th and 90th percentile marks was considered significant. In the marsh loss portion of the model, changes in timing of marsh loss of 10 or more weeks were considered significantly different.

The numbers of nutria reported for this analysis are the mean stable population sizes for the last 61 weeks of the simulation, after population parameters such as birth rates, mortalities, and gestation periods are bal-

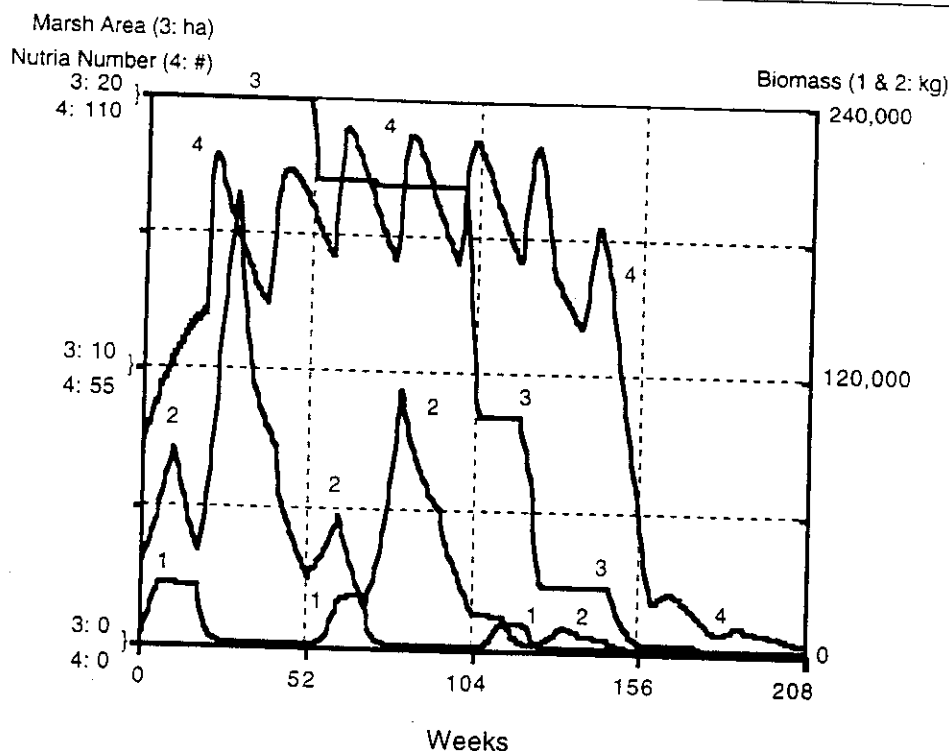


Figure 3. Standard nutria-biomass-area model results. Key: (1) biomass of *Scirpus americanus* in kg, (2) biomass of *Spartina patens* in kg, (3) vegetated marsh area in hectares, (4) numbers of nutria.

anced. The model implicitly assumes that the population is closed and that there are no food or nutria population density-dependent interactions. The exception to this assumption is when the model is run using a nutria population density-dependent impregnation rate. In those instances the population density is calculated for 20 ha. Unless otherwise noted, simulations were conducted for 5 years; in all cases, the population reached some dynamic equilibrium.

RESULTS

Nutria-Biomass-Area Model Behavior

The simulation model run under standard parameters predicts a rise in nutria numbers from an initial 40 nutria to 92 nutria and then a population collapse after the area of marsh declines to near 0 (Figure 3). The biomass for *Scirpus* and *Spartina* fluctuates over the annual cycle, with declining peaks as the total area of marsh decreases, until the biomass collapses as the marsh area decreases to near 0. In the nutria-biomass area model, marsh area decreased in a stepwise fashion during seasonal biomass lows (Figure 3). With each incremental drop in marsh area, the maximum amount of *Spartina patens* decreased while the number of nutria remained stable. Nutria populations did not show a significant response to the decrease in plant biomass until after marsh area dropped to less than 5 hectares.

Biomass-Area Model Behavior

The biomass model and area model were run unlinked from the nutria model as the "biomass-area model" to demonstrate model performance with "no nutria." The biomass varied between 29,175 kg and 203,025 kg for *Spartina patens* and between 200 kg and 28,975 kg for *Scirpus americanus*. The marsh area did not change when the biomass-area model was run under standard conditions. Since the biomass model was fitted directly from the data, no sensitivity analysis was performed on its parameters.

Nutria Model Behavior

The nutria model was run unlinked from the biomass model and area model to determine a baseline for nutria population dynamics. When the nutria model is run by itself, the nutria population has a size but not a density. Using standard model parameters, the population reached a dynamic equilibrium at 92 nutria, or 4.6 nutria/ha. We performed sensitivity analyses on the nutria model to determine the effects of juvenile and adult survivorship, impregnation rate, young-per-female, and lag times on model performance.

When annual adult survivorship was varied from 5% to 80%, the mean stable population size varied between 69.5 and 161.9 nutria (Figure 4a). When the juvenile annual survivorship was varied from 5 to

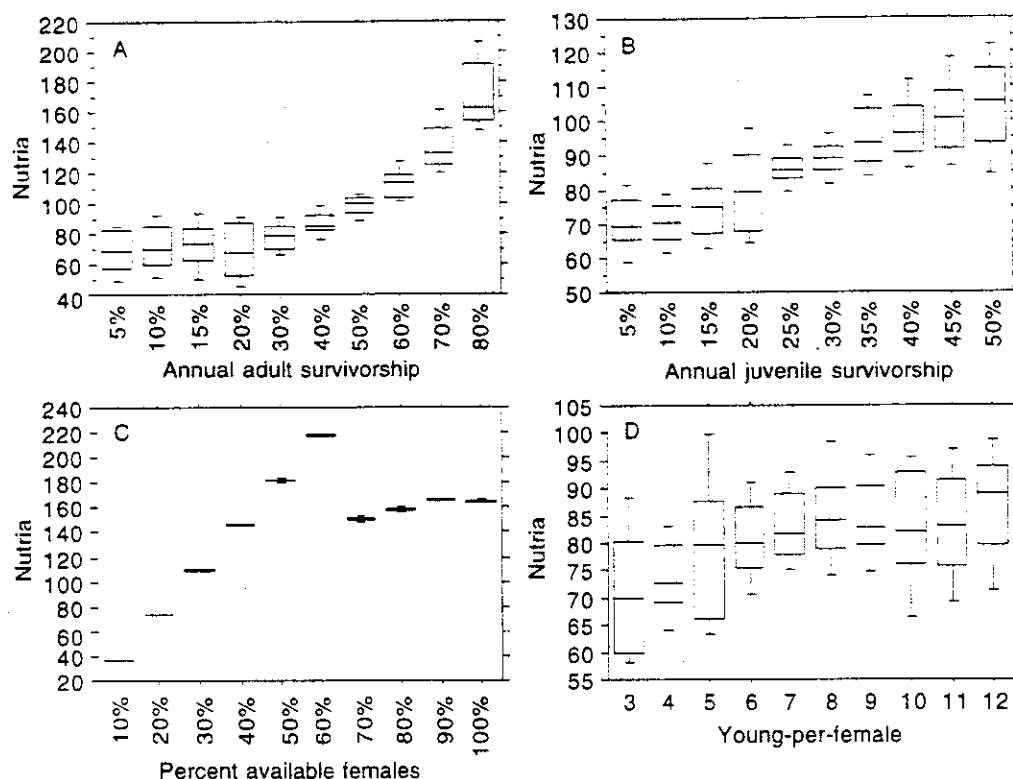


Figure 4. (A) Effect of adult survivorship on population size. (B) Effect of juvenile survivorship on population size. (C) Effect of impregnation rate on population size. The percentage of available females that became pregnant during each time step was held constant during these simulations. (D) Effect of litter size on population size. The horizontal bars (from bottom to top) represent the values for the 10th, 25th, 50th (mean), 75th, and 90th percentiles respectively. These values were calculated from the weekly population numbers for the last 61 weeks of a 5-year simulation run.

50%, the mean population size varied between 60.8 and 105.2 (Figure 4b).

To examine the effects of impregnation rate, we set the impregnation rate (which normally was density dependent) to be a constant. We varied it from 10 to 100% of available females. The population in response varied between a mean of 37.3 and 220 (Figure 4c).

The population sizes increased with increasing impregnation rate to a population high of 220 nutria at a 60% impregnation rate. Impregnation rates greater than 60% resulted in smaller population sizes of around 160 nutria.

We varied the young-per-female from 3 to 12. The resultant population size varied between 70.0 and 89.6 (Figure 4d). We also varied the young-per-female at higher than standard survivorships. More than 7 young-per-female did not significantly increase the dynamic equilibrium population mean but did significantly increase the variance (Figure 5).

Varying the gestation period from 15 weeks to 23.1 weeks varied the population size between 76.3 and 82.6 (Figure 6). We varied the weeks-to-maturity from 10 to 50 weeks (Figure 7). Although the mean number of nutria varied between 80 and 92, the overlap in the

standard deviations and lack of clear trends in average numbers indicated that varying the gestation period and weeks-to-maturity did not significantly affect mean nutria numbers in the nutria model.

We varied adult and juvenile survivorship and young-per-female together to replicate the high nutria population densities reported in the literature. After 5 years at the highest survivorships and young-per-female, the population averaged 72 nutria/ha (Figure 8).

Sensitivity Analysis of Nutria-Biomass-Area Model

We performed sensitivity analyses on the nutria-biomass-area model. We examined the effects on model performance of the type of marsh loss equation used, parameters used in the marsh loss model, nutria survivorships, impregnation rates, and food per nutria requirement.

Changing the marsh loss equation changed the time to total marsh loss by less than 20 weeks, and the response curves for time versus hectares of marsh were almost identical. We varied the critical density at which marsh loss began from 1100 kg/ha to 2000 kg/ha and examined the time it took the marsh to be re-

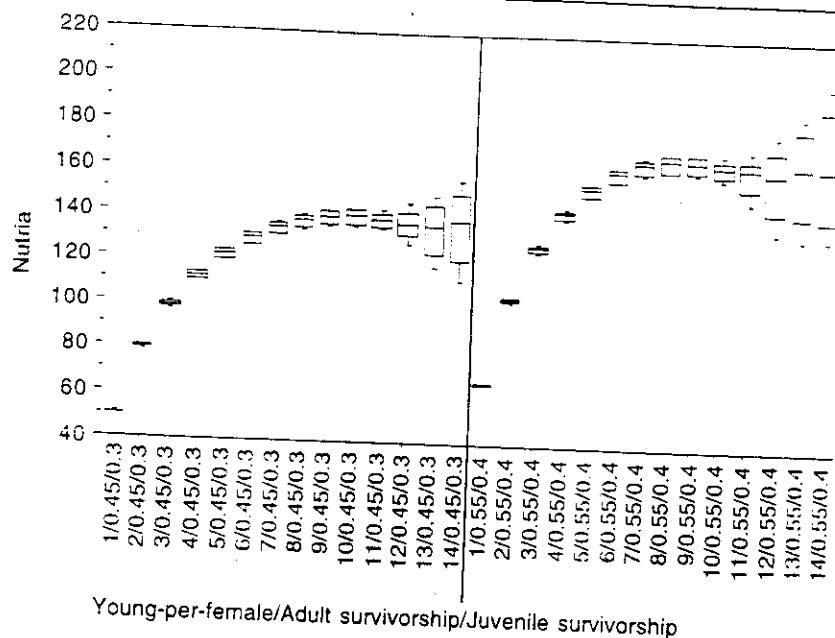


Figure 5. The effect of simultaneously varying litter size, adult survivorship, and juvenile survivorship on the population size. The horizontal bars (from bottom to top) represent the values for the 10th, 25th, 50th (mean), 75th, and 90th percentiles. These values were calculated from the weekly population numbers for the last 61 weeks of a 5-year simulation run.

ed to approximately 10% of its original amount. re was less than one year's difference between the two extremes. The shapes of the response curves for time versus hectares were almost identical, the chief difference being that biomass was shifted up with lower critical densities.

Varying the food requirement per nutria in the nutria-biomass-area model had a significant effect on the time to marsh collapse (Table 2). The maximum feeding rate at which marsh loss did not occur in the nutria-biomass-area model was 74.6 kilograms per nutria per

week. We next varied the biomass requirement with the area model unlinked from the biomass model and nutria model. The nutria-biomass model became stable when the biomass requirement per nutria was reduced to 71 kg or less per nutria per week.

Varying adult survivorship delayed the nutria population crash by less than 20 weeks. The exception was when adult survivorship was set at 25% and juvenile survivorship was set at 20%. At these low combined survivorships, the time to population crash was advanced by approximately 80 weeks. We varied weeks-to-maturity in the nutria-biomass-area model (Figure 9). It did not affect whether the system collapsed, but it did affect the timing of system collapse. No simple pattern was apparent between weeks-to-maturity and time to collapse; however, intra-annual variability changed with weeks-to-maturity.

DISCUSSION

The nutria model predicts a stable population density of 92 nutria or 4.6 nutria/ha in a closed population. This density is within the range of population densities reported in the literature but well below the high estimates of 21.4 and 43.7 nutria/ha (Willner 1982, Kinler et al. 1987). We did achieve the high population densities in our model in as little as 2 years, but we had to adjust survivorship parameters significantly upward. This adjustment implied either that survivorships as measured in the field are lower than actual

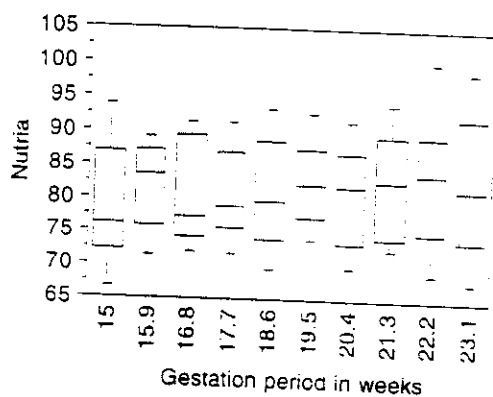


Figure 6. Effect of gestation period on population size. The horizontal bars (from bottom to top) represent the values for the 10th, 25th, 50th (mean), 75th, and 90th percentiles, respectively. These values were calculated from the weekly population numbers for the last 61 weeks of a 5-year simulation run.

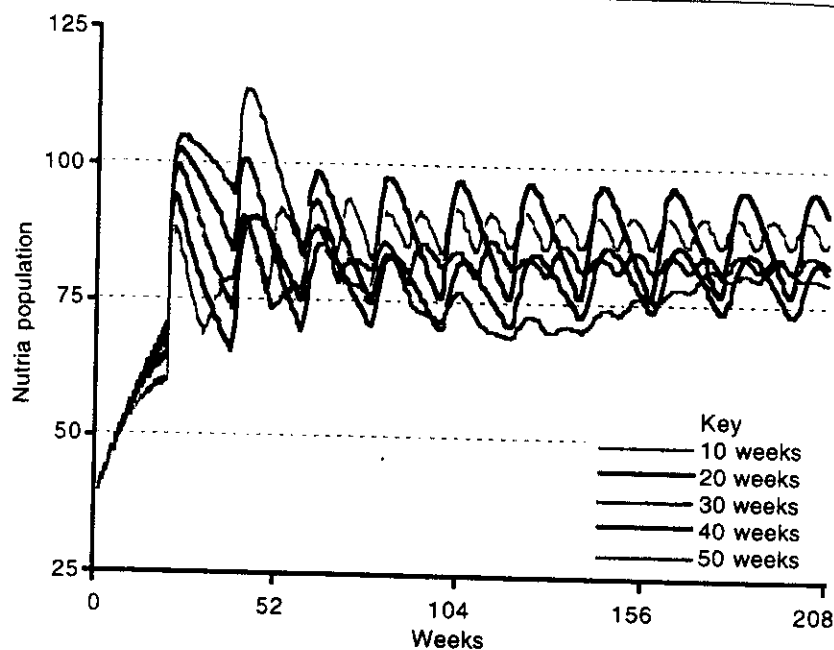


Figure 7. Effect of varying weeks-to-maturity on population size. Note that while the population sizes stay within 25 individuals of each other, the variance and wave frequency vary substantially.

nutria survivorship or, alternatively, that population densities are lower than the estimates. Yet another explanation could be that nutria survivorship is not constant but varies with the quality of the environment. High survivorship may allow for a quick growth in the

population, thus reaching high densities. At high population densities, resources may become limited, leading to an increase in mortality. If population densities and survivorships were measured at peak population times, it could give the skewed impression that nutria

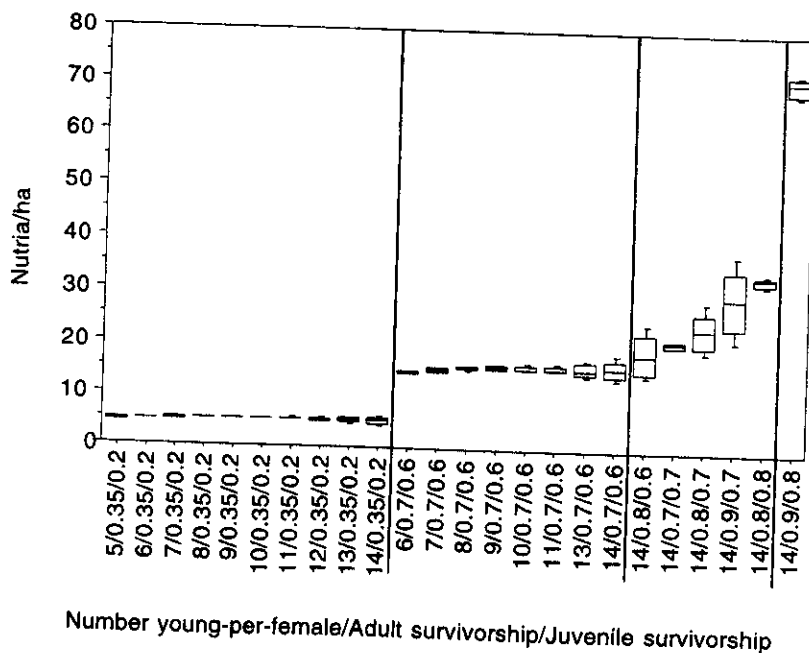


Figure 8. Effect of simultaneously varying litter size and survivorship on population density. Our goal with this set of simulations was to see what survivorships were necessary to achieve the highest population densities reported in the literature (e.g., Willner 1982, Kinler et al. 1987). The horizontal bars (from bottom to top) represent the values for the 10th, 25th, 50th (mean), 75th, and 90th percentiles, respectively. These values were calculated from the weekly population numbers for the last 61 weeks of a 5-year simulation run.

Table 2. The effect of nutria food requirement in the nutria-biomass-area model on weeks until marsh area collapse. The amount of food per nutria was varied and the number of weeks until population collapse observed. The week of collapse was arbitrarily defined as the week when the population dropped to approximately 5% of the maximum population during the simulation. The standard value used in the model is indicated with an asterisk "**".

Kilograms/nutria/week	Week of Population Collapse
204	100
183	106
161	121
140	149
96.25*	203
83	260
77	422
≤74.6	stable

can sustain high population densities even in the face of high mortality.

Much of the population variability in the nutria model can be attributed to the density-dependent nature of the impregnation rate. When impregnation rates were held constant, population sizes showed little or no variance. It is also interesting to note that the population size reached a peak at a 60% impregnation rate and then dropped to a stable level at higher impreg-

nation rates. This result indicated an optimal impregnation rate for population growth and a saturation effect.

The parameters that we know best are those that can be obtained from captive nutria populations, including gestation period, young-per-female, and to a lesser extent, time to maturity. Unfortunately the model was not particularly sensitive to these parameters. The unlinked nutria model is most sensitive to survivorship and least sensitive to time-based parameters.

The nutria-biomass-area model was most sensitive to the nutria weekly biomass requirement and not particularly sensitive to the marsh loss model used once loss of marsh began. The collapse of the nutria-biomass model indicated that the model system was not supportable, even in the absence of eat-out related losses of marsh area. This conclusion, however, is very sensitive to the level of biomass loss per nutria that we assumed. The importance of critical density was determined by the level of the weekly biomass requirement. At very low and very high biomass requirements, critical density was not important. At intermediate levels of weekly nutria biomass requirements, the critical density could determine whether the system crashed.

While weeks-to-maturity did not significantly affect equilibrium population sizes in the nutria model, it did significantly affect time-to-collapse in the nutria-bio-

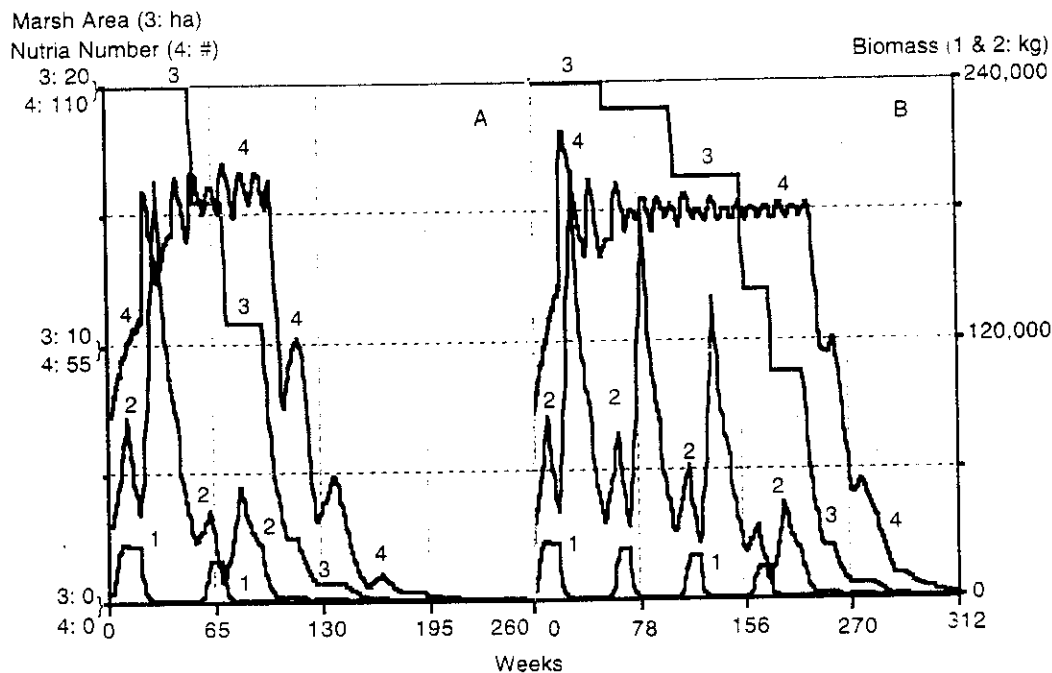


Figure 9. Effects of varying weeks-to-maturity in the nutria-biomass-area model. The biomass of *Scirpus americanus* (1), *Spartina patens* (2), vegetated marsh area (3), and nutria numbers (4) are compared using two different weeks-to-maturity: 10 weeks (A) and 30 weeks (B). Plant biomass is in total kilograms, marsh area is in hectares, and nutria population size is in total number of nutria.

mass-area model. The difference between the sensitivity of the nutria model and the nutria-biomass-area model to weeks-to-maturity was because intra-annual variation of population size could place nutria numbers at levels that caused rapid loss of marsh at critical times. Thus, high variance, not mean numbers, was driving the sensitivity of the nutria-biomass-area model to weeks-to-maturity.

The seasonal timing of marsh loss in the nutria-biomass-area model, during winter biomass lows, fits our field observations. In the nutria-biomass-area model nutria do not cause a loss of marsh area most of the year. It is during seasonal biomass lows that the nutria biomass demands can exceed sustainable levels. Since this is a very short time, however, the nutria population does not respond fast enough to the seasonal food loss. The slow nutria population response allows nutria populations to be maintained at or near the nutria's natural equilibrium levels until the marsh-area base completely collapses. Consequently, if we want to manage nutria numbers to minimize their impact on marsh, we should try to obtain optimum population densities prior to winter when the marsh is most susceptible to damage. Estimates of the carrying capacity of the marsh should be made during the seasons when the marsh is most vulnerable to loss through nutria herbivory.

We made two important assumptions in our nutria model. First, the nutria model is a closed population model, while nutria populations in the wild are generally open to migration. Second, we did not include "random" events that can cause a rapid drop in population, such as winter kills (Linscombe et al. 1981, Kinler et al. 1987). Gosling et al. (1983) created a population dynamics model to explore the effects of winter kill and found that successive severe or mild winters could lead to four-fold changes in the population. Winter kills occur during the same time of year that our nutria-biomass-area model indicated that nutria damage the marsh.

Our model indicates that information is needed on the biomass that nutria need per capita (including waste) and under what circumstances their feeding activities lead to a breakup of the marsh. It also suggests that improvements in the estimates of population sizes and survivorships might be needed.

Starfield (1997) stated that model building has utility beyond making predictions and that the process of model building itself is useful in formulating hypotheses and exploring alternative hypotheses. In that spirit, our model has tied literature data on nutria population dynamics to our work on marsh plant phenology. Furthermore, we have discovered discrepancies between reported population dynamics parameters and model performance, and we have identified knowledge

gaps pertaining to per-capita nutria impacts and marsh loss dynamics. Because important parameters in our model are unknown or doubtful, our model should not be used for population management; however, we now know which parameters must be obtained, the relative importance of those parameters, and what directions future models should take.

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LITERATURE CITED

- Arwood, E. L. 1950. Life history studies of nutria, or coypu, in coastal Louisiana. *Journal of Wildlife Management* 14:249-265.
- Carter, J., A. L. Foote, and L. A. Johnson. 1998. Nutria model. U.S. Geological Survey, National Wetlands Research Center, <http://www.nwrc.usgs.gov/nutria/readme.htm>
- Coreil, P.D. 1976. Habitat preferences, movements, and activities of adult female nutria in a southwestern Louisiana intermediate marsh area. M.S. Thesis. Louisiana State University, Baton Rouge, LA, USA.
- Ehrlich, S. 1962. Two experiments in inducing nutria aggregation in unfenced artificial ponds. *Hydrobiologia* 19:316-333.
- Evans, J. 1970. About nutria and their control. Bureau of Sport Fisheries and Wildlife, Denver, CO, USA. Resource Publication 86.
- Foote, A. L. and L. A. Johnson. 1993. Plant stand development in Louisiana coastal wetlands: nutria grazing effects on plant biomass. p. 265-269. In M.C. Landin (ed.) *Wetlands: Proceedings of the 13th Annual Conference of the Society of Wetland Scientists*, New Orleans, LA. South Central Chapter, Society of Wetland Scientists. Utica, MS, USA.
- Gosling, L. M., S. J. Baker, and J. R. Skinner. 1983. A simulation approach to investigating the response of a coypu population to climatic variation. *EPPO Bulletin* 13:183-192.
- Gosling, L.M. and S. J. Baker. 1989. Demographic consequences of differences in the ranging behavior of male and female coypus. p. 155-224. In R.J. Putman (ed.) *Mammals as Pests*. Chapman and Hall, New York, NY, USA.
- Harris, V. T. and F. Webert. 1962. Nutria feeding activity and its effect on marsh vegetation in southwestern Louisiana. U. S. Fish and Wildlife Service, Washington, DC, USA. Special Scientific Report Wildlife 64.
- High Performance Systems Inc. 1994. STELLA II, High Performance Systems Inc., Hanover, NH, USA.
- Johnson, L. A. and A. L. Foote. 1997. Vertebrate herbivory in managed coastal wetlands: a manipulative experiment. *Aquatic Botany* 59:17-32.
- Kinler, N. W., G. Linscombe, and P. R. Ramsey. 1987. Nutria. p. 327-343. In M. Novak, J. Baker, M. Obbard, and B. Malloch (eds.) *Wild Furbearer Management and Conservation in North America*. The Ontario Trappers Association, Toronto, Ontario, Canada.
- Linscombe, G., N. Kinler, and V. Wright. 1981. Nutria population density and vegetative changes in brackish marsh in coastal Louisiana. p. 129-141. In J. A. Chapman and D. Pursley (eds.) *Proceedings of the Worldwide Furbearer Conference*, Frostburg, MD, USA.
- Linscombe, G. and N. Kinler. 1997. A Survey of Vegetative Damage Caused by Nutria Herbivory in the Barataria and Terrebonne Ba-

- sins. Barataria-Terrebonne National Estuary Program. Nicholls State University, Thibodaux, LA, USA.
- Newson, R. M. 1969. Population dynamics of the coypu, *Myocastor coypus* (Molina), in eastern England, p. 203-204. In K. Petrusewicz and L. Ryszkowski (eds.) *Energy Flow through Small Mammal Populations*. IBP Publishers, Oxford, UK.
- Nowak, R. M. (ed.) 1991. *Walker's Mammals of the World*, 5th Edition, Volume 2. John Hopkins University Press, Baltimore, MD, USA.
- Reggiani, G., L. Boitani and R. De Stefano. 1995. Population dynamics and regulation in the coypu *Myocastor coypus* in central Italy. *Ecography* 18:138-146.
- Starfield, A. M. 1997. A pragmatic approach to modeling for wildlife management. *Journal of Wildlife Management* 61:261-270.
- Willner, Gale R. 1982. Nutria, p. 1059-1076. In J. A. Chapman, and G. A. Feldhammer (eds.) *Wild Mammals of North America*. John Hopkins University Press, Baltimore, MD, USA.

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