Bayesian analysis of deer reproductive condition

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Abstract: A hunting program was instituted in a previously un-hunted 836-ha county park in New Jersey for white-tailed deer (*Odocoileus virginianus*) in 1994. Harvested deer were aged and weighed. The reproductive tracts of female deer were examined and the number of embryos counted. Hierarchical Bayes modeling was used to examine whether or not compensatory reproduction was occurring in the park. Compensatory reproduction is an issue which is frequently raised by anti-hunting groups.

Contents

1. Introduction

Compensatory reproduction is an increase in wildlife reproductive rate as habitat condition improves. This phenomenon is frequently cited as a reason to forego a hunting program. Hunting opponents argue that following harvest, reproduction rates of the residual animals will increase (due to the decreased population density), and perhaps eventually culminate in a population that is larger and in poorer physical condition than the one present prior to harvesting. In support of this thesis, it has been documented that when deer are in poor physical condition, reproductive rates may increase as the physical condition of deer improves. For instance, in a 252-ha enclosure in Michigan, [11] found in utero productivity of yearling does doubled

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TABLE 1
Number of deer harvested annually during study.

yr	total number harvested
1994	88
1995	50
1996	167
1997	185
1998	169
1999	118
2000	53
2001	50
2002	47
2003	—
2004	99
2005	82
2006	57
2007	70
2008	56

with supplemental feeding and increased by 50% among 2.5-year-olds and 21% for older does. [18] found that productivity may decrease with increasing deer density even when supplemental feed is available and [15] found that fertility rates of deer in urban areas may be influenced by population density and physical condition.

This study takes advantage of a unique opportunity to study potential changes in reproductive rates of a previously un-hunted deer population. Hunting was prohibited in the Watchung Reservation in northern New Jersey for at least one hundred years. During the 1980s, the number of neighboring homeowners complaining of deer (*Odocoileus virginianus*) damage to backyard gardens increased, as did the number of deer - vehicle accidents on roads surrounding the Reservation. Noticeable damage to the native plant community was observed in the Reservation. As a result, deer hunts were held annually from 1994–2008, with the exception of 2003 (Table 1). Data were collected on harvested deer during each year of the program. Each deer was aged, and the sex and weight recorded. For pregnant does, the number of embryos and corpora lutea was also recorded.

We examined whether reproductive rates and weights of harvested deer varied over the course of the program. If average weights and reproductive rates increased, this might suggest that compensatory reproduction ([9, 14, 2]) has occurred in the park. Our objective was to determine if reducing the deer population at the Watchung Reservation in Union County, New Jersey, led to an improvement in the physical condition, as measured by a trend of increasing weight, and/or female reproductive rates of harvested deer.

2. Hierarchical Models

We use Bayesian Hierarchical modeling in this study. These are models in which the parameters in the prior distribution for the data model are themselves assigned prior distributions. The parameters in the prior are called hyperparameters, and the prior(s) for the hyperparameters are usually termed hyperprior distributions (*e.g.* see [7]).

In non-Bayesian modeling, models are categorized as either fixed or random effects models depending on whether or not the experimental subjects are assumed to have been randomly drawn from a larger population or not, and whether interest focuses on the specific subjects in the experiment, or on the population from which

those subjects were drawn (*e.g.* see [4]). In Bayesian hierarchical modeling, this distinction is unnecessary. In Bayesian modeling, the terms random effects and fixed effects are not often used, since even fixed effects are not *fixed* according to the Bayesian paradigm. However, Bayesian models often appeal to a related concept known as exchangeability. Suppose there are k experimental units, y_i, $i = 1, 2, \ldots, k$. Individual y_i's are said to be exchangeable if the probability density $p(y_1, y_2, \ldots, y_k)$ is invariant to permutations of the subscripts of the y_i's (*e.g.* see [1] or [7]). In practical terms, this means that there is nothing distinctive about any of the individual y_i's, and all the subscript i does is separate data on one subject from another.

In principle, there is no limit to the number of levels in a hierarchical model. The appropriate number of levels of prior distributions to specify varies from problem to problem. However, as mentioned in [3], typically there is little advantage to adding additional priors beyond the second-stage prior, or what we called the hyperprior above. The reason for this is that data are usually relatively non-informative for parameters above the hyperprior level, and adding additional levels of prior structure generally results in only very small changes to the posterior distributions of the parameters at the data model or (first) prior distribution level.

3. Data collection

Volunteer agents brought harvested deer to a deer check station located in the Reservation. The deer were weighed and, for females, the number of corpora lutea in the ovaries and number of embryos in the uterus were counted. Deer were aged using a tooth eruption and wear technique [12]. The number of deer harvested, by year is displayed in Table 1. The average number of embryos per year, by age class is shown in Table 2. Finally, Table 3 shows the average weight (*kg*) of harvested deer, by age class, for each year of the study.

4. Analyses

4.1. Reproduction rate model

The response variable of interest in the reproduction study was y_{ijk}, the number of embryos observed in animal k in age class i at year j; $i = 1, 2, 3$; $j = 1, 2, \ldots, 15$; $k = 1, 2, \ldots, n_{ij}$; n_{ij} = number of animals observed in age class i at year j. The

TABLE 2
Reproductive Rates (embryos per doe) of deer harvested, sample size in parentheses.

	fawn	yearling	adult
1994	0.00 (12)	1.50 (16)	1.51 (39)
1995	0.00 (4)	1.29 (7)	1.71 (14)
1996	0.25 (24)	1.52 (29)	1.92 (54)
1997	0.06 (31)	1.37 (27)	1.85 (52)
1998	0.21 (34)	1.60 (23)	1.91 (46)
1999	0.58 (24)	2.00 (14)	2.11 (18)
2000	0.50 (2)	1.80 (9)	1.50 (6)
2001	0.33 (3)	1.63 (8)	2.00 (6)
2002	0.00 (7)	2.00 (8)	2.20 (5)
2003	—	—	—
2004	0.20 (10)	1.50 (20)	1.90 (20)
2005	0.40(5)	1.50 (10)	1.90 (21)
2006	0.50 (4)	1.40 (5)	2.00 (6)
2007	0.38 (13)	2.00 (8)	1.87 (15)
2008	0.75 (8)	1.60 (5)	1.80 (10)

TABLE 3
Weight (kg) of fawns, yearlings and adult deer harvested during study.

	male			female		
	fawn	yearling	adult	fawn	yearling	adult
1994	24.5	42.2	45.8	21.8	38.1	42.3
1995	25.1	41.8	47.3	19.2	34.7	36.1
1996	27.6	38.8	46.9	24.5	35.7	40.8
1997	26.4	38.5	43.7	24.4	37.1	40.0
1998	26.9	42.2	46.6	24.6	39.4	40.5
1999	29.7	42.5	49.7	27.9	39.9	42.8
2000	30.6	45.7	46.2	26.9	36.9	37.5
2001	25.2	35.8	47.5	20.9	30.4	35.2
2002	28.9	45.7	56.8	25.9	38.9	43.8
2003	–	–	–	–	–	–
2004	23.8	42.6	45.2	23.4	36.2	41.0
2005	25.9	40.9	48.9	25.7	36.0	37.1
2006	35.2	48.7	52.8	28.9	41.8	47.2
2007	28.8	44.4	45.2	25.0	34.9	35.2
2008	25.7	42.2	37.2	23.5	33.3	39.3

observed covariate was j, the year in which the animal was observed. The latter variable assumed an integer value between 1 and 15 (there were 15 years in the study). Since the response variable was a count variable, we posited a generalized linear model with a Poisson likelihood and logarithmic link function to account for heterogeneity of the Poisson parameter (*e.g.* see [5, 6, 10, 17]). In order to see if there was a trend in the number of embryos per age class over the study period, the link function was modeled as linear function of study year.

Six candidate models were identified and fitted to the embryo data. The candidate models were:

$$(4.1) \qquad \begin{array}{c} y_{ijk} \sim \text{Pois}\left(\lambda_{ij}\right); \ \ln\left(\lambda_{ij}\right) = \beta_{0i} + \beta_{1i}j \\ \beta_{li} \sim \text{N}\left(\theta_l, \tau_l^2\right); \ \theta_l \sim \text{N}\left(0, \ 1 \times 10^6\right); \ \tau_l \sim \text{Unif}\left(0, \ 100\right); \ l = 0, 1 \end{array}$$

$$(4.2) \qquad \begin{array}{c} y_{ijk} \sim \text{Pois}\left(\lambda_{ij}\right); \ \ln\left(\lambda_{ij}\right) = \beta_{0i} + \beta_{1i}j \\ \beta_{li} \sim \text{N}\left(0, \tau_l^2\right); \ \tau_l \sim \text{Unif}\left(0, \ 100\right); \ l = 0, 1 \end{array}$$

$$(4.3) \qquad \begin{array}{c} y_{ijk} \sim \text{Pois}\left(\lambda_{ij}\right); \ \ln\left(\lambda_{ij}\right) = \beta_{0i} + \beta_{1i}j \\ \beta_{li} \sim \text{N}\left(0, \ 1 \times 10^6\right); \ l = 0, 1 \end{array}$$

$$(4.4) \qquad \begin{array}{c} y_{ijk} \sim \text{Pois}\left(\lambda_j\right); \ \ln\left(\lambda_j\right) = \beta_0 + \beta_1 j \\ \beta_l \sim \text{N}\left(0, \tau_l^2\right); \ \tau_l \sim \text{Unif}\left(0, \ 100\right); \ l = 0, 1 \end{array}$$

$$(4.5) \qquad \begin{array}{c} y_{ijk} \sim \text{Pois}\left(\lambda_i\right); \ \ln\left(\lambda_i\right) \sim \text{N}\left(0, \tau^2\right) \\ \tau \sim \text{Unif}\left(0, \ 100\right) \end{array}$$

$$(4.6) \qquad \begin{array}{c} y_{ijk} \sim \text{Pois}\left(\lambda\right); \ \ln\left(\lambda\right) \sim \text{N}\left(0, \tau^2\right) \\ \tau \sim \text{Unif}\left(0, \ 100\right) \end{array}$$

Models 4.1, 4.2, and 4.3 include age-class effects (different intercepts and slopes for each age-class) and a time trend. These models differ in the structure of their prior distributions. Model 4.4 includes a time trend, but no age-class effects. Model 4.5 includes age-class effects, but no time trend, and Model 4.6 does not include age-class effects or a time trend.

Model 4.1 is a full hierarchical model. In this model the β_{li}'s were assigned normal priors, and the means and variances of those priors were in turn assigned vague hyperpriors. In Model 4.2, the priors for the β_{li}'s were normal, with mean 0 and unspecified variances. The latter parameters were assigned vague hyperpriors. Hence in model 4.1, the β_{li}'s were shrunk toward a common mean (θ_l), implying that intercept and slope for each age class were realizations from common underlying distributions (one for β_0 and one for β_1). Under model 4.2, the β_{li}'s were all shrunk towards 0. In model 4.3, the β's were assigned vague priors and no hyperpriors were specified. Hence under model 4.3, no shrinkage across age classes occurred. The prior specifications for Models 4.4, 4.5, and 4.6 were derived from the specification of model 4.2.

The hyperpriors for the prior standard deviation (τ or τ_l, depending on the model) were assigned vague priors. Experimentation with different specifications indicated that the upper bound (100) had no appreciable effect on the results.

All the models were fitted to the reproduction data (678 observations) with WinBUGS, ver. 1.4.3 [8]. Trial runs confirmed that all the models converged to their posterior distributions in fewer than 70,000 iterations. Each model was run for 100,000 iterations, and DIC [13] was computed for each model using iterations 90,001–100,000. We also examined a pseudo-r^2 measure for each model, in order to get a sense of how well the models fitted the data. For the latter statistic, we divided the sum of squared residuals by the usual corrected total sum of squares on each iteration. The average of this ratio over the final 10,000 iterations was then computed.

4.2. Weight model

We hypothesized that the weight of harvested animals varied linearly over time, and that the time trend varied by sex and age class. This was formalized with the following model:

$$(4.7) \qquad w_{isjk} = \beta_{0is} + \beta_{1is}j + e_{isjk}, \ e_{isjk} \sim \mathrm{N}\left(0, \sigma^2\right),$$

where w_{isjk} was the weight (kg) of deer k in age class i and sex s, and year j. One again, the latter assumed an integer value between 1 and 15. Age classes were coded as 1= fawn, 2 = yearling and 3 = adult, and sex was coded as 1= male and 2 = female. Hence the index k assumed the values 1, 2, …, n_{isj}, where n_{isj} was the number of deer observed in age class i and sex s at year j.

To complete the model, we required prior distributions for β_{0is} and β_{1is}, the model coefficients for age class i and sex s. We were more comfortable specifying priors for the weight model and proceeded as follows: β_{0is} represents the mean 1993 weight for a deer in age class i, of sex s. We postulated that the expected 1993 weight of fawns was certainly between 0 and 46 kg, with a mean of roughly 23 kg. Since the range of a normal distribution is roughly 6 standard deviations in length, we found τ_{011} and $\tau_{012} = 43/6 = 7.2$. To be conservative, we increased these to $\tau_{011} = \tau_{012} = 10$, where τ_{011} and τ_{012} are the prior standard deviations of β_{011} and β_{012}, respectively. Hence τ_{011}^2 and $\tau_{012}^2 = 100$. Thus the prior distributions for β_{011} and β_{012} were:

$$\beta_{011} \sim \mathrm{N}\left(23, 100\right), \ \beta_{012} \sim \mathrm{N}\left(23, 100\right).$$

We applied the same reasoning to the mean 1993 weights for yearlings and adults, postulating mean 1993 weights of 34 and 45 kg, respectively, and the same variances

as were used for the fawn weights. This led to the following prior distributions:

$$\beta_{021} \sim \text{N}\,(34, 100)\,,\ \ \beta_{022} \sim \text{N}\,(34, 100)\,,$$
$$\beta_{031} \sim \text{N}\,(45, 100)\,,\ \ \beta_{032} \sim \text{N}\,(45, 100)\,.$$

We also imposed the constraints $\beta_{031} \geq \beta_{021} \geq \beta_{011}$ and $\beta_{032} \geq \beta_{022} \geq \beta_{012}$, i.e., in 1993, for each sex, adults weighed more than yearlings, and yearlings weighed more than fawns.

Under model (4.7), the slopes β_{1is} represent annual rate of change in mean weight for age class i and sex s. We postulated that the largest value we would expect for a slope would be 1.5, and the lowest would be -1.5. Accordingly, we let (-1.5, 1.5) be the range for the slopes, which led to standard deviations of 0.5 and variances of 0.25. Hence we specified the following prior distributions for the slopes:

$$\beta_{1is} \sim \text{N}\,(0, 0.25)\,,\ \ i = 1,\ 2,\ 3;\ \ s = 1,\ 2.$$

We investigated a number of other, noninformative prior specifications for β_{0is} and β_{1is}, including adding another level to the model hierarchy. In each case, the model estimates were nearly identical to the ones resulting from the specification detailed above.

In order to determine whether age class and sex effect were necessary, we also fitted models without these effects:

No sex effects:

$$(4.8) \qquad w_{isjk} = \beta_{0i} + \beta_{1i}j + e_{isjk},\ \ e_{isjk} \sim \text{N}\left(0, \sigma^2\right),$$

$$\beta_{01} \sim \text{N}\,(23, 100)\,,\ \ \beta_{02} \sim \text{N}\,(34, 100)\,,\ \ \beta_{03} \sim \text{N}\,(45, 100)\,,\ \ \beta_{1i} \sim \text{N}\,(0, 0.25)\,.$$

No age class effects:

$$(4.9) \qquad w_{isjk} = \beta_{0s} + \beta_{1s}j + e_{isjk},\ \ e_{isjk} \sim \text{N}\left(0, \sigma^2\right),$$

$$\beta_{0s} \sim \text{N}\,(34, 100)\,,\ \ \beta_{1s} \sim \text{N}\,(0, 0.25)\,.$$

We assumed the vague prior $\sigma^2 \sim \text{IG}(0.001, 0.001)$ for each weight model. As in the reproduction model, model adequacy was evaluated using DIC. Initial runs revealed that the models converged very quickly ($<$10,000 iterations). Hence each model was run for 50,000 iterations, and DIC was computed from the final 10,000 iterations. We also computed a pseudo-r^2 for each model.

5. Results

5.1. Reproduction rate model

The DIC values for models 1–6 were 1548.21, 1549.29, 1547.59, 1839.63, 1552.54, and 1839.84, respectively. The pseudo-r^2 values were 0.596, 0.588, 0.600, 0.011, 0.574, and 0.002, respectively. Hence models 1–3 (and possibly 5) were the best, but there was no clear support for any particular model. Since model 3 had the fewest parameters (as well as the lowest DIC), we chose model 3 as the appropriate model for the reproduction data. Hence our analysis indicated that both age-class and yearly trend effects were important. The pseudo-r^2 value indicates that the model fit reasonably well, accounting for 60% of the variation in embryos observed in harvested females.

TABLE 4
Means and lower (2.5%) and upper (97.5%) bounds for 95% credibility intervals from marginal posterior distributions, for parameters in reproduction model.

parameter	mean	2.5 percentile	97.5 percentile
β_{01}	-2.033	-2.647	-1.469
β_{02}	0.345	0.119	0.568
β_{03}	0.541	0.397	0.681
β_{11}	0.096	0.033	0.159
β_{12}	0.015	-0.013	0.043
β_{13}	0.011	-0.009	0.011
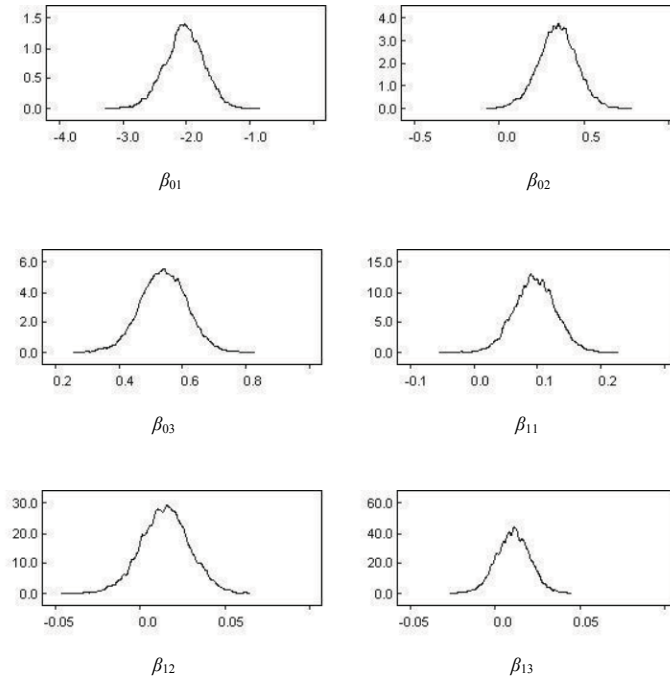
FIG 1. *Marginal posterior distributions for parameters in reproduction rate model*

Model 3 was run for an additional 10,000 iterations and then the means and approximate 95% credibility intervals were computed for each parameter from the joint posterior sample using the final 10,000 iterations. If there was significant time trend, we would expect the 95% credibility intervals for β_{11}, β_{12}, and β_{13} to exclude zero. Examination of the credible intervals (Table 4) and the smoothed kernel density estimates of the marginal posteriors for the parameters (Figure 1) showed that the 95% credibility interval for β_{11} (slope for fawns) did not include zero, whereas the intervals for β_{12} and β_{13} (slopes for yearlings and adults, respectively) did. This indicated that reproduction rate did change over time (increase) for fawns, but not for yearlings or adults.

5.2. Weight model

The DIC values were 6697.65, 6918.09, and 7955.77, for models 7, 8, and 9, respectively. The pseudo-r^2 values were 0.704, 0.630, and 0.038, respectively. Clearly model 7 was best supported by the data and both age-class and sex effects were

Table 5

Means and lower (2.5%) and upper (97.5%) bounds for 95% credibility intervals from marginal posterior distributions, for parameters in weight model.

parameter	mean	2.5 percentile	97.5 percentile
β_{011}	26.29	25.52	27.82
β_{012}	23.90	22.48	25.30
β_{021}	40.15	38.43	41.85
β_{022}	37.78	36.35	39.22
β_{031}	46.17	43.69	48.63
β_{032}	41.25	39.55	42.89
β_{111}	0.0752	−0.0689	0.2207
β_{112}	0.1288	−0.0514	0.3103
β_{121}	0.3304	0.1506	0.5120
β_{122}	−0.1186	−0.3075	0.0709
β_{131}	0.1912	−0.1064	0.4908
β_{132}	−0.1880	−0.4158	0.0392
σ^2	27.15	24.93	29.55

important. Again, the pseudo-r^2 value indicates that the model fit reasonably well, accounting for 70% of the variation in deer weights. This model was run for an additional 50,000 iterations and then the means and approximate 95% credibility intervals were computed for each parameter from the joint posterior sample using the final 50,000 iterations. In addition, the marginal posterior distributions for each parameter were computed. The 95% credible intervals for the model parameters (Table 5) and the smoothed kernel density estimates of the marginal posteriors (Figure 2) revealed that the only slope corresponding to a 95% credible interval that did not include zero was β_{121}, the slope for yearling males. Hence there was a significant trend (increase) in weight for yearling males, whereas there were no significant trends for any other sex-age class combination during the study period.

6. Discussion

In 1994, the year of the first hunt, the average weights of deer indicated that the herd was in standard or above standard physical condition. With the exception of yearling male weights, the physical condition (the weights of deer by gender and age) did not change significantly in the fifteen years since the first hunting program. The reproductive rates of yearling and older does at Watchung Reservation did not increase as the number of deer in the Reservation decreased. However the reproductive rate of fawns increased.

Compensatory reproduction, an increase in the reproductive rate as the condition of wildlife improves, is frequently cited as a reason not to conduct a hunting program. Some hunting opponents suggest that hunting should never be allowed because as the condition of the herd improves, the reproductive rates will increase, and the deer population will grow. In the case of Watchung Reservation, the deer were initially in good physical condition. Reducing the number of deer in the Reservation did not reduce competition for a limited food source, as evidenced by the fact that the physical condition of the deer (the weight) did not improve. Reproductive rates of the yearling and adult deer did not increase with a reduction of the deer population. However, the reproductive rate of the female fawns increased from 0% in the first years of the deer reduction program to over 30% in years 12 through 15 of the hunt, resulting in a significant linear annual trend. [11] and [16] found an increase in productivity as the physical condition of the deer improved, and [15] found deer fertility rates to be influenced by population density or physical
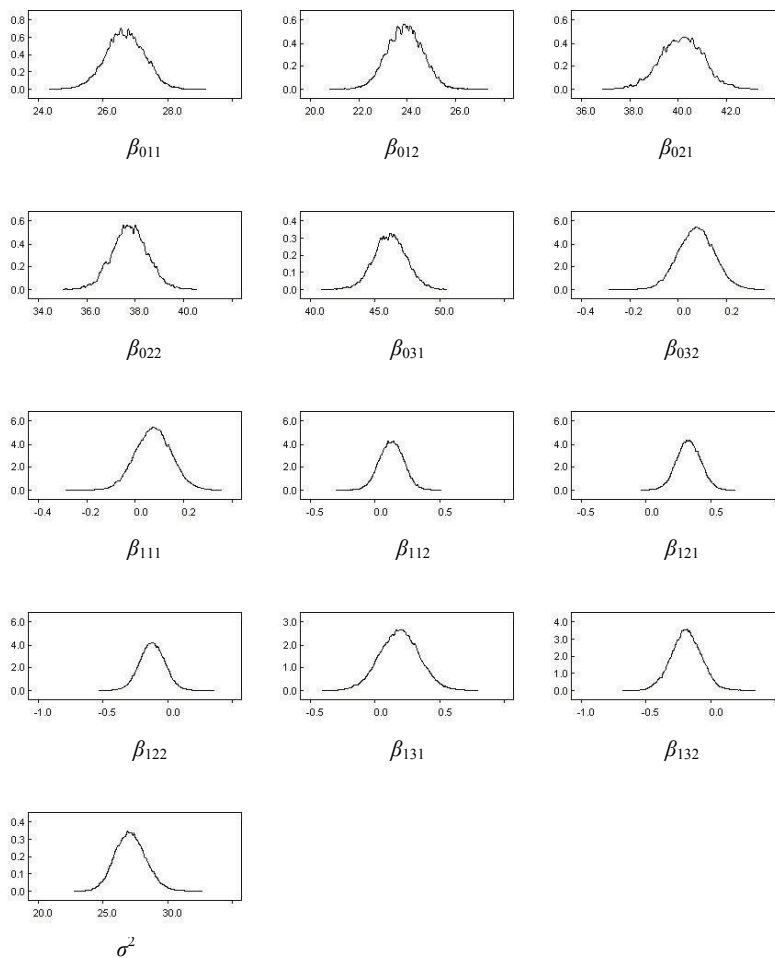
FIG 2. *Marginal posterior distributions for parameters in weight model*

condition in urban areas. Our results differ somewhat from these findings because the physical condition of the deer at Watchung Reservation remained unchanged for five of the six age class-sex combinations studied, and the reproductive rates of two of the three age classes examined did not change over time.

Acknowledgements

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