

From fertility control to population control: improving efficacy of deer immuno-contraception programs.

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ABSTRACT: The recent application of immunological agents for wildlife contraception holds promise for yet another tool for managing overabundant deer populations. Yet, little is known about the effects of these kinds of contraceptives on free-ranging herds. Here, we report on a small free-ranging deer population that has been treated with porcine zona pellucida (PZP) for that last five years. Our direct involvement began over three years ago when we conducted monthly density and herd composition profiles. Despite five years of treatment, our observations are that the population is not decreasing and some fawns continue to be born into the population every year. In addition, there appears to be two birth pulses in the study population – one during late May and early June, and the other occurring in August and September. We propose several plausible mechanisms to account for these observations, and explore them in detail using simulation models. We attribute the observed response to a combination of technological difficulties of vaccine delivery, to a population-scale sampling problem, and to dose-related problems associated with polyestrous breeders like white-tailed deer. Finally, we suggest changes in the current treatment protocol that could alleviate most if not all difficulties with achieving a zero birth rate.

Interest in the application of fertility control for ungulate population management has been revived through the development of immunological contraceptive agents like porcine zona pellucida (PZP; Kirkpatrick et al. 1996). However, studies documenting the use of PZP on captive white-tailed deer (*Odocoileus virginianus*) have suggested that PZP may extend the breeding season as treated females continue to ovulate through ≥ 3 estrous cycles (McShea et al. 1997, Turner et al. 1992, 1996). A protracted breeding season could result in two potentially negative outcomes. First, because breeding males may lose up to 30% of their autumn body mass through nutritional deprivation in a “typical” breeding season (Moen and Severinghaus 1981, Holzenbein and Schwede 1989), extending the breeding season for an additional 2-3 months could prove fatal, particularly if the ensuing winter is harsh. Second, depending upon the dose administered, some females may actually be breeding late in the season as blood antigen levels fall below the contraceptive threshold, which is indicated by a later than typical birth pulse. In this latitude, overwinter fawn survival is determined in large measure by birth date (Moen and Severinghaus 1981), and fawns born 2-3 months late are not likely to survive even a mild winter.

To date, very little has been done in either of these problem areas, and conclusions reported are equivocal at best (McShea et al. 1997). This report was precipitated through work conducted on a population of deer which has been subjected to PZP treatments for 5 years (Underwood et al. 1998). In particular, two observations have arisen from detailed population

and herd composition estimates: (1) despite 5 years of treatment, this population is not declining. In fact, there is compelling evidence that it is growing, albeit at a slow rate, and (2), there appears to be a bimodal birth pulse with fawns being born in late May and again in August, approximately 12 weeks later.

Hyperbole surrounds both sides of the efficacy issue, and these observations portend serious political and biological implications regarding the use of PZP for controlling free-ranging deer populations. That said, objectives of this report include the exploration of plausible mechanisms that might account for our observations and to identify areas of uncertainty in the current treatment protocol which could be bolstered to mitigate any problems identified. In particular, we develop a population profile over the period of interest, build a model to simulate delivery of PZP vaccine to the number of females indicated in the profile, and evaluate the major assumptions inherent in its construction and use. Our goal is simple — to move the state of the technology from fertility control to population control.

Study Area

Fire Island is a barrier island located along the southern coast of Long Island, New York (40 41' N, 73 00' W). It is approximately 51 km long and averages about 0.5 km in width. The island is bordered by the inlets of Fire Island to the west and Moriches to the east, and is separated from Long Island by Great South and Moriches Bays (Fig. 1). The physiognomy of Fire Island is typical of Atlantic barrier islands, which grade from a primary dune along the ocean to salt marsh along the bay. Dominant vegetation includes pitch pine (*Pinus rigida*), beach grass (*Ammophila breviligulata*), wax myrtle (*Myrica cerifera*), bayberry (*M. pensylvanica*), shadbush (*Amelanchier canadensis*), and common greenbrier (*Smilax rotundifolia*). This particular composition of vegetation is typical of Fire Island except within the various communities where residents have planted non-indigenous vegetation.

Located throughout the western half of Fire Island are 17 towns and villages. Access to these communities is provided by boat or by vehicle via the Robert Moses Causeway. The Burma Road, a vestige of abandoned development plans, bisects the island along its entire length and represents the focus of restricted vehicular traffic within the towns and villages of Fire Island. However, the Burma Road is largely impassable along sections between adjacent communities. A network of boardwalks is common within most Fire Island communities and serves as the primary thoroughfare for predominantly pedestrian and bicycle traffic. The villages from the western edge of Kismet to the western edge of Lonelyville (K-L) comprise the primary study area (Fig. 2).

An attempt has been made by volunteer “monitors” to identify every female deer in the study area on the basis of individual markings so that a history of fertility could be developed on each deer. Over the last 5 years, the Humane Society of the United States (HSUS) has overseen the treatment of these deer.

We assume in this analysis that every female had undergone the initial 2-shot protocol (see Kirkpatrick et al. 1996), which includes a primary vaccine treatment and a follow-up booster shot, prior to the start of this study.

Methods

Population profiles for the K-L study area were generated from monthly density and herd composition estimates reported in Underwood et al. (1998) for 1995, 1996 and 1997. Point estimates of population density were derived from an un-weighted regression of density on time for the study area using July of each year as the point of reference. The estimated number of deer was computed by multiplying the density by 1.6 km^2 (i.e., size of the K-L study area), and the estimated number of females was computed by multiplying by the average percentage of females in herd composition counts made from July-December of each year. The profile for 1997 was constructed by using herd composition estimates from the months of June, September and February (1998). The number of neonatal (< 1 month old) fawns in each year was estimated similarly, except that total fawn production was partitioned into those born during the expected birth pulse and those born later. We used the average proportion of neonatal fawns observed during July-August counts as the best estimate for the former, and the difference in the average proportions observed in September-December and July-August for the latter, assuming no neonatal mortality.

To explore issues surrounding the identification of individual females, a simulation model was constructed, which accepts as its primary input, the number of females to be treated in the population (Fig. 3). The model then creates the desired number of females as records in a database and initializes two traits for each doe: (1) a logical flag indicating whether or not she has been vaccinated, and (2), a placeholder indicating the total number of vaccinations she has received during the period of treatment. Because each deer is assumed to have already undergone the initial 2-shot protocol during the first year, a single booster shot is all each female is supposed to receive in subsequent years. Note that this expectation is predicated upon knowing the identity of each deer without error. Erroneous identification would allow some deer to potentially receive more than one shot during each treatment period.

Next the process of encountering and treating a female is simulated through a simple sampling experiment. For the accurate identification scenario, the sampling is conducted without replacement. For all other scenarios, the degree of replacement is determined by comparing a random number (rn) drawn from the uniform distribution $[0,1]$ and the probability of correct identification (p_{id}). If the female is incorrectly identified (i.e., $rn > p_{id}$), a booster shot is administered regardless of her recent history of treatment. The sampling is governed by 2 additional constraints. First, an average daily treatment rate (dtr) must be specified, and sets a limit to the total number of females vaccinated on any given day. Second, the total treatment duration (ttd) must also be specified and, in combination with dtr , sets an upper limit to the total number of females that can be treated.

Two models of selecting samples are implemented. The first is a “random encounters” model, where a record (i.e., female) in the database is drawn at random and then subsequently dispatched. All subsequent samples are drawn in the same manner. In reality, treatment more likely proceeds in a systematic fashion once the first group of females is encountered. While the initial encounter with the first female may be random, the probability of treatment for other females in the group (if there are any) will be much higher, thus violating the assumption of random sampling. We simulate this case by randomly selecting the first record (i.e., female), then test each subsequent female in order until the number of females indicated by *dtr* is achieved. We refer to this case as the “non-random encounters” model.

Estimates of *dtr* and *ttd* were obtained from unpublished data reported in memoranda of the HSUS. For simplicity, we initiated all simulations assuming 100% accuracy in the identification of individual females. Other scenarios were modeled to illustrate potentially useful insights for improving treatment efficacy. For example, with the random encounters model, we ran a series of factorial-like simulations altering *dtr* and *ttd* for populations of 50, 100, 200 and 400 females to explore the effect of sampling error on the probability of receiving at least 1 vaccination. We used simple plots and regression to summarize the results of these simulations.

We then ran simulations in which the fraction of females correctly identified varied from 0.5-1.0 to explore the impacts of misidentifying individual females on treatment efficiency. In these simulations, the model stipulates that no matter how uncertain the identity of individual deer, no female could be given more than a single vaccine in the same day. On subsequent days, however, a previously vaccinated deer might not be correctly identified and could be vaccinated again. We report the mean fraction (No. simulations = 30) of the female population receiving none, 1, 2, or 3 vaccinations over the specified treatment period.

Results

Estimated density increased from about 77-93 deer km⁻² from July 1995-98 (Fig. 4), an increase of about 25 deer on the study area. While the regression was statistically significant ($P < 0.01$), the fit was poor ($R^2 = 31\%$) indicating high variation in density over time.

Population profiles constructed from mean herd composition counts (Table 1) and density estimates indicate between 71-96 yearling and adult females occupying the K-L study area over the 3 year period (Table 2). Estimates of about 4 neonatal fawns observed in the early summer were consistently predicted over time. In general, about twice as many neonates appear in late summer surveys than in early summer surveys, indicating a period of births during August and perhaps the first couple of weeks in September. Overall, the average conception rate over the three year period was 12.8%.

In a memo dated 14 January, 1998, an HSUS biologist reported treating 207 deer with the PZP vaccine over a 30 day period. This effort translates into a *dtr* = 7 deer, and *ttd* = 30 days. Assuming 100% accuracy in identifying deer and about 300 females throughout western Fire Island, the random encounters model suggests that a third of all females will receive no vaccine (Table 3). That fraction does not change using the non-random encounters model so long as

identification is perfect. Uncertainty in identification of individual deer results in the non-random encounters model producing a slightly (~30%) higher fraction of deer which do not receive a booster shot.

The fraction of females failing to receive a vaccination increases at a rate which diminishes inversely with the female population size when identification is certain. The intercepts of this family of curves are negative, indicating that the probability of missing females declines to zero at a certain *ttd* or *dtr* (Fig. 5). Doubling *dtr* or *ttd* produces the same effect on the fraction of deer not receiving a vaccine, greatly improving efficacy at the population level.

The proportion of the total female population receiving more than one vaccination increases as identification accuracy declines (Table 3). For example, if identification is 70% accurate (i.e., 3 of 10 females are incorrectly identified), just under 40% of all females will receive no vaccine, just over half of all females receive one vaccination, and just under 10% of all females receive >1 vaccine. At accuracies poorer than 0.7, the probability of receiving >1 booster shot becomes non-trivial.

Discussion

Given the estimated number of fawns born in last several years, it is certainly possible that the deer population is growing, albeit at a slow rate. Divining plausible mechanisms to account for this fact is not an easy task when considering the number of potential factors involved, however. Nevertheless, the overall increase of about 25 deer is entirely accounted for by the estimated fawn recruitment (i.e., 31 deer), mortality notwithstanding. However, without knowing those losses specifically, this exercise is moot. More importantly, perhaps, is understanding why the population is not declining.

The population reconstruction suggests that the percentage of females conceiving is declining; however, some females are: (1) not being vaccinated in the previous autumn, (2) not showing antigenic response to the PZP vaccine, or (3) not being contracepted due to other causes (e.g., dart failed to deliver a full dose). The simulations indicated that by increasing either *dtr* or *ttd* substantially reduces or eliminates the probability of failing to vaccinate some females, suggesting that more effort is required to ensure that every deer gets at least one shot. While this explanation is the most parsimonious, it certainly is not the only one. In reality, all three failure mechanisms are likely affecting efficacy in combination.

The two models of deer encounters predict a fraction of missed females that lie on either end of estimates from the population reconstruction, which suggests that actual encounters with female deer is not a purely random or systematic process. Somewhat surprising is that the non-random encounters model exacerbates rather than alleviates the sampling problem. This simulation was designed to approximate how baiting deer to a focal location affects treatment of deer. The simple manner in which this process was simulated falls short of reality, however. Visiting different bait stations on subsequent days, increasing *dtr*, or both, would likely smear the difference between the two models.

Nevertheless, considering that the increase in the fraction of missed females between the models was ~33%, a critical reevaluation of how baiting is used to increase efficacy should be made.

The population reconstruction also suggests that the majority of conceiving females are breeding late in the season. Backdating an average 202-day gestation for white-tailed deer on Long Island (Jackson and Hesselton 1973) identifies an active period of breeding for these females between the end of January and the middle of February. We suggest that these are females receiving some PZP, but whose antigen levels are falling below the threshold for contraception late in the breeding season.

As evidence in support of this argument, we offer several additional facts: (1) every other study of PZP-contracepted deer has reported late-breeding in females not exhibiting titers above the contraceptive threshold (Turner et al. 1992, 1996, McShea et al. 1997); (2) in an unpublished study, we observed a significant difference in the proportion of active scrapes maintained by adult male deer in the study area and a control area during February and March, but not in November and December of 1994-95; and (3) we have accumulated several anecdotal observations of males mounting females during February, including males who already had shed their antlers.

It appears that under current protocols, implications for the use of PZP for managing overabundant deer herds are severe, from both philosophical and pragmatic viewpoints, particularly in northern climates where a high proportion of late-born fawns would surely perish, even during mild winters. A naive view suggests that by ensuring that all females get enough PZP to effectively contracept them for the entire breeding season, these problems will go away. This view is complicated by a number of factors, however.

First, depending upon the realized accuracy of identification of female deer, some females may already be receiving 2 vaccinations, which clouds an analysis of the efficacy of a single treatment booster. In other words, is the efficacy of a single booster shot really 87% (i.e., 100-13%), or perhaps lower? Second, which 13% of the female population is exhibiting this response? An analysis of the treatment and response histories of individual females should provide insight as to whether this is more generally a dose-related problem, or one focused on a subset of females that just do not show a strong antigenic response to PZP.

Our limited perspective suggests three areas where further investigation may prove fruitful. First, a population decline cannot be effectively achieved unless zero fertility *is* the population goal – and can only be achieved if every female of reproductive age is vaccinated. Mechanisms affecting efficacy at the individual level contribute, but do not account entirely for lowered efficacy at the population level. We believe an important sampling problem arises when the goal is population control. Greater effort than has been expended in the past is needed to improve efficacy at this level. Increasing the number of females treated each day, or increasing the time spent treating females greatly improves the probability of vaccinating every deer. Because time is usually the limiting constraint, increasing the number of people actually administering the vaccine is the most plausible way to overcome this hurdle.

Second, evaluating the efficacy of the current protocol is not possible unless or until the number of vaccinations each female receives can be determined without error. This evaluation is critically tied to correct identification of females, which under the present system is not perfect. We cannot determine from our data if there is a dose problem in general, or whether the fawns we see in August and September are born to specific dames who do not exhibit a sufficient antigenic response to PZP. One potential solution is to ensure that all females undergo a 2-shot treatment regime every year, which has already been alluded to in the literature (Turner et al. 1996). To guard against errors in identification, a mark-and-inject darting system might be used indiscriminately until encounters with untreated females falls below some acceptable level.

Finally, none of this analysis would have been possible without a scientifically acceptable method of assessing population size and herd composition. We feel strongly that our method, while far from perfect, represents the best way to collect these data in a timely manner. We urge that any future research endeavor on Fire Island have, as a principal component, a rigorous plan of routine population monitoring and periodic analysis of population status.

Acknowledgments

We wish thank the many people who assisted us, particularly James P. Fischer, who nearly single handedly conducted the density and herd composition surveys. Dr. Mary K. Foley provided funding for this work. Michael Bilecki contributed valuable logistical support, additional funding, and ran administrative interference for us so we could get on with the work at hand.

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Table 1. Herd composition estimates (% of total population) for the Kismet-Lonelyville study area, Fire Island, New York.

Year	% ♀♀(SE) July-December	% Fawns (SE) July -August	% Fawns (SE) September-December
'95	0.57(0.016)	0.03(0.005)	0.10(0.006)
'96	0.63(0.017)	0.03(0.020)	0.08(0.005)
'97	0.65(0.036)	-	0.05(-)

Table 2. Reconstructed population of deer in the Kismet-Lonelyville study area, Fire Island, New York. Estimates are derived from routine surveys of density and herd composition.

Year	Density (No. km ⁻²)	No. Deer	No. Does	Fawns in Early Summer‡	Fawns in Late Summer	Total Fawns	% Does† Conceiving
'95	77.2	124	71	4	9	13	18.3
'96	84.9	136	86	4	7	11	12.8
'97	92.6	148	96	-	-	7	7.3
Difference =		24			Sum =	31	

‡ earliest pre-treatment birth was 920525; latest recorded birth was 920621 (unpubl. data).

† assumes a negligible twinning rate; pre-treatment (1992) conception estimates were 60% with a 33% twinning rate among dames (unpubl. data).

Table 3. Proportion of females receiving vaccinations of PZP under different assumptions about the accuracy of identifying individual deer. The random encounters model was used with an initial female population size of 300, $dtr = 7$ and $tt_d = 30$. All values are means of 30 simulations.

Probability of Correct Identification	Proportion (%) Receiving Vaccinations		
	0	1	2
1.0	30	70	0
0.9	35	61	5
0.8	38	56	6
0.7	40	52	8
0.6	41	49	9
0.5	44	44	11

Figure 1. Location of Fire Island National Seashore including the Kismet-Lonelyville (K-L), Fire Island Pines (FIP), Fire Island Wilderness Area (FWA) and the William Floyd Estate (WFE) study areas.

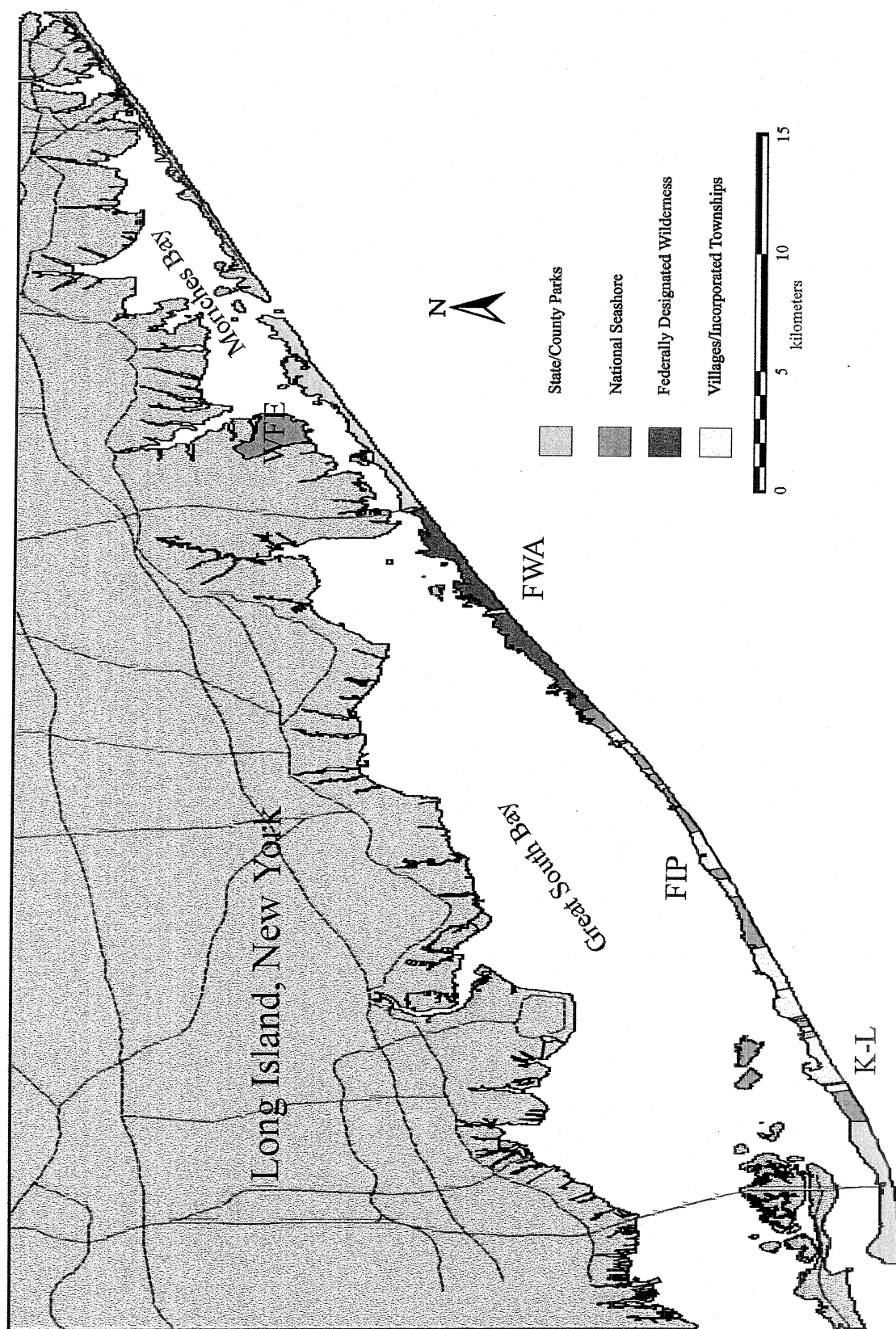
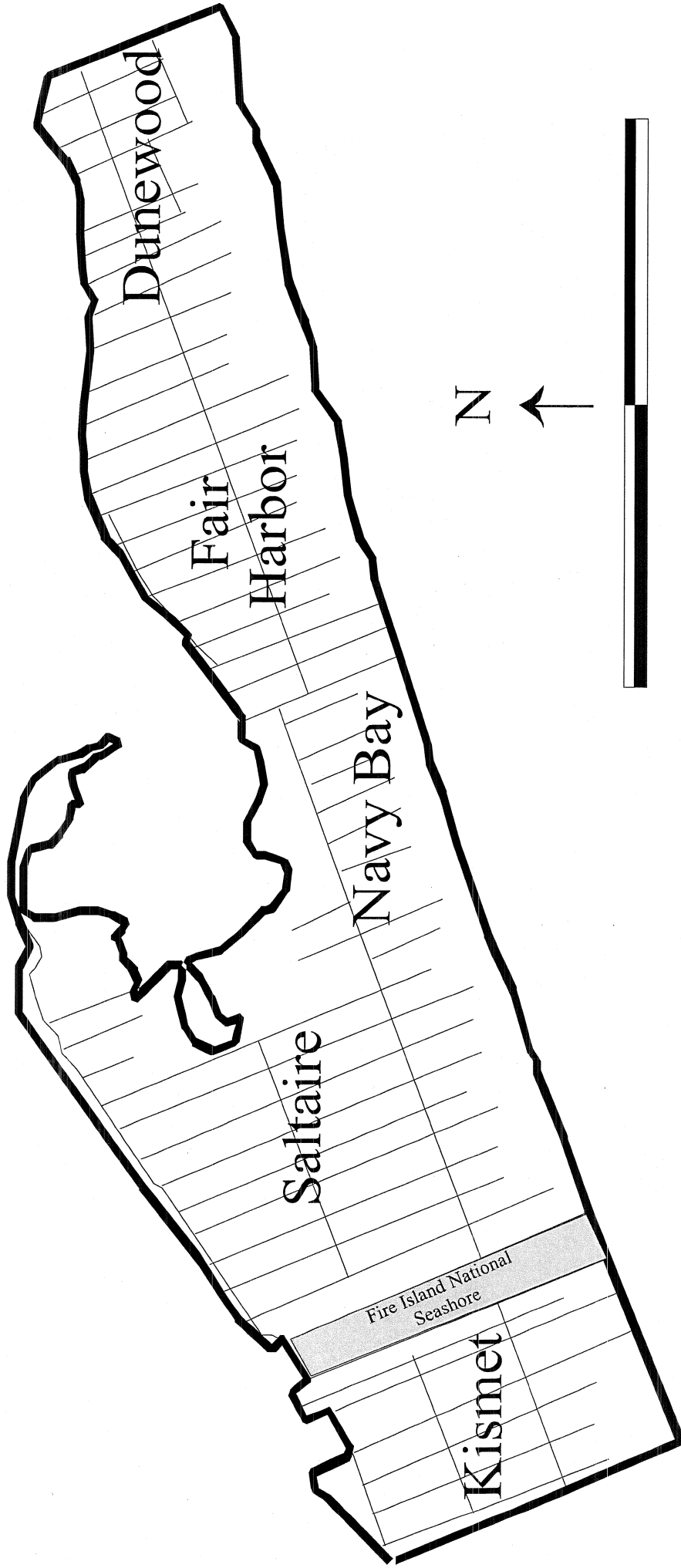


Figure 2. Kismet-Lonelyville (K-L) study area and associated localities, Fire Island National Seashore, New York. The area of K-L is approximately 1.6 km².

Great South Bay



N

0 1 Kilometers

Atlantic Ocean

Figure 3. Schematic of control flow logic of a computer program designed to simulate the process of administering PZP-vaccine to any given number of female deer. The program exploits the dBase III+ file format and programming language, and simulates 2 separate sampling designs. The program uses several third party add-ons to the dBase III+ language.

USER INPUT

Input:

Females (n)

Prob. of Correct ID (p_{id})

Avg. Daily Treatment Rate (dtr)

Total Treatment Duration in Days (ttd)

Simulation Runs ($nsims$)

Start

Runs = 0

Create Data
Structure

Days = 0

Deer = 0

Runs = Runs+1

Days = Days+1

Deer = Deer+1

Draw Random
Number (1,n)
(rn)

Move File Pointer
to Record = rn

Treated
Today?

Draw Random
Number (rn)
 $0 \leq rn \leq 1$

+ ID?
 $rn \leq p_{id}$

Change Status
Treated = .T.

Need
Booster?

Vaccines =
Vaccines + 1

Vaccines =
Vaccines + 1

Change Status
Treated = .T.

deer <
 dtr ?

C

DOEPOP.DBF

Record #	Treated	Vaccines
1	.F.	0
2	.F.	0
3	.F.	0
.	.	.
n	.F.	0

Random
Encounters
Process

See Non-Random
Encounters
Process

B

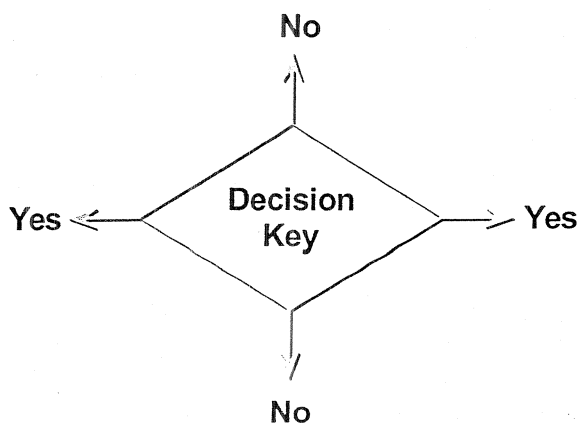
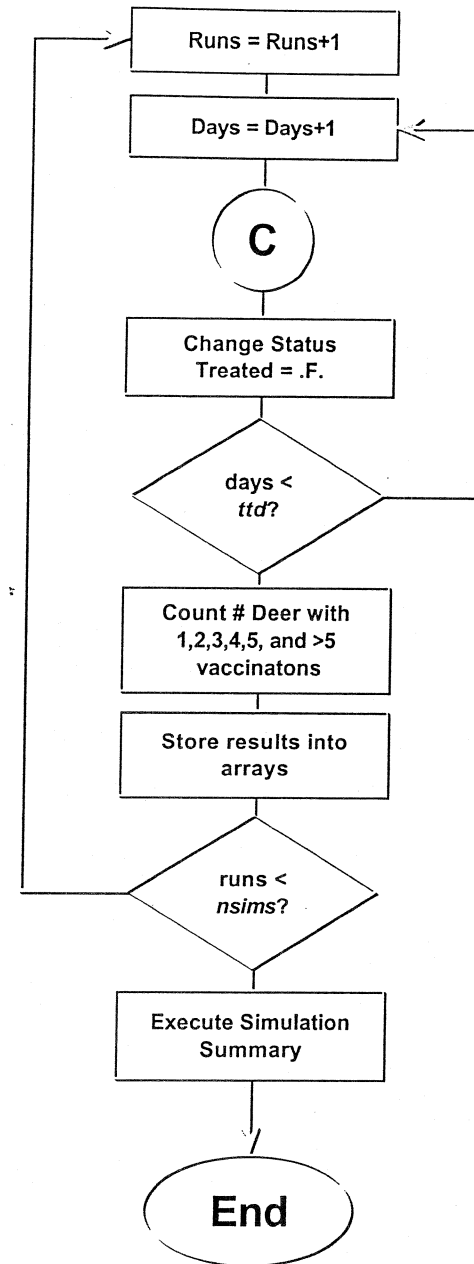
Decision
Key

Yes

Yes

No

No



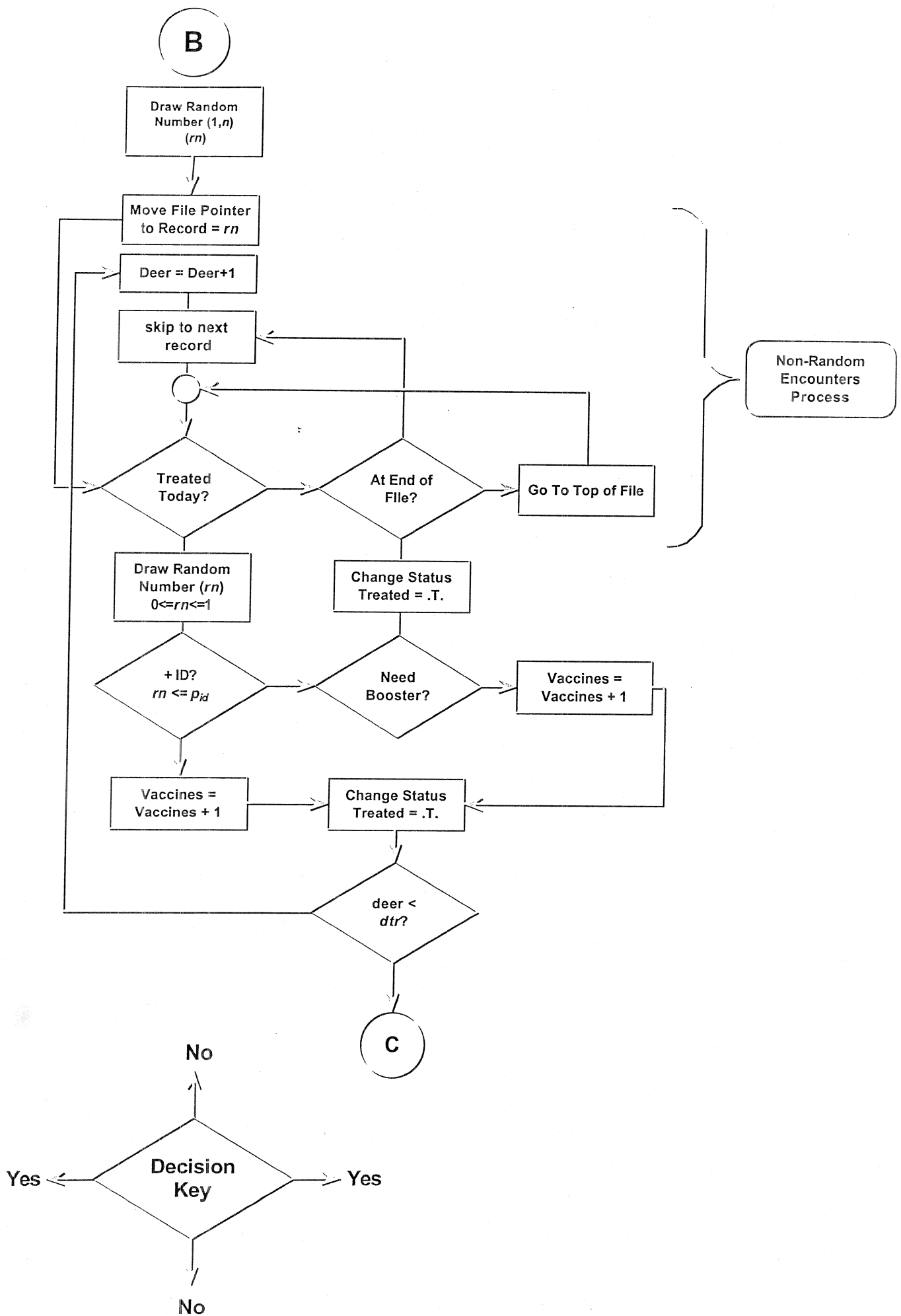


Figure 4. Monthly density estimates of white-tailed deer on the Kismet-Lonelyville study area, Fire Island, 1995-98. Upper panel includes the regression of mean density (variance ignored) on time, excluding November, 1995 and August, 1996 (see Underwood et al. 1998).

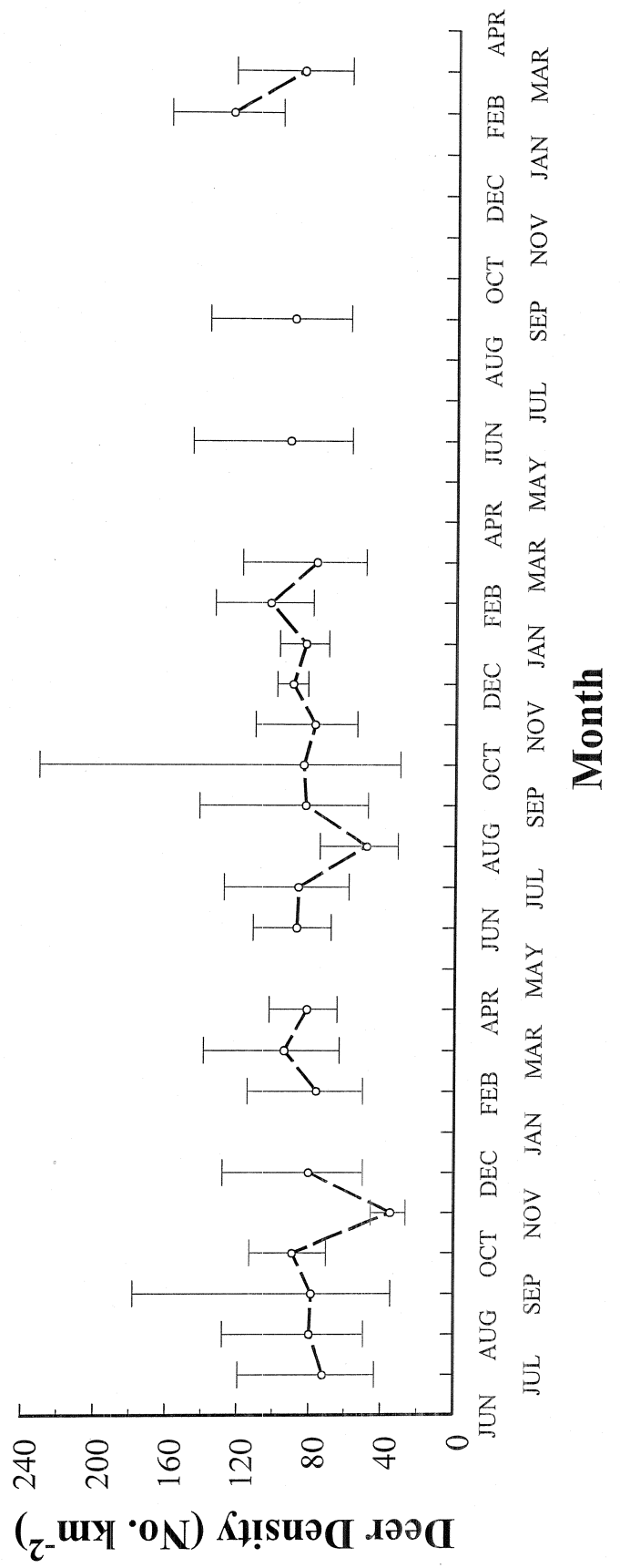
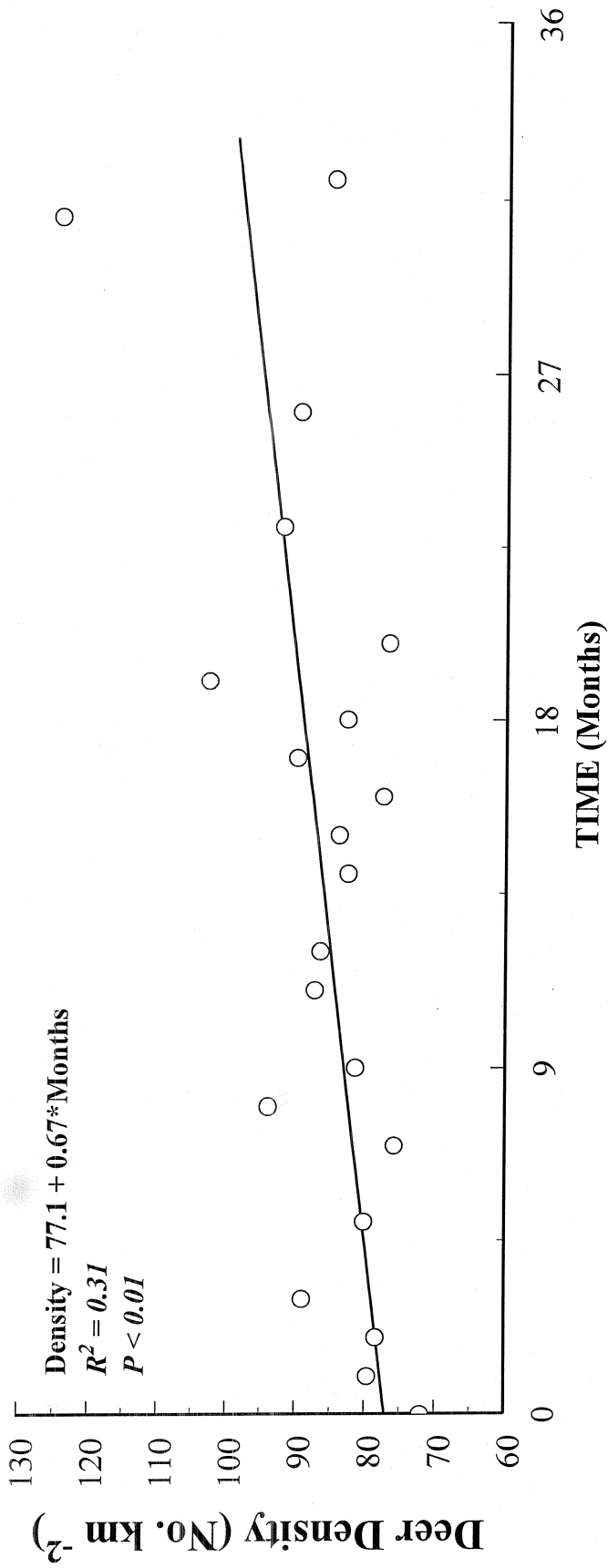


Figure 5. Relationship of female population size and the fraction of females not receiving a booster vaccine by chance alone, constrained by a daily treatment rate over a specific treatment duration.

