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CATCH-EFFORT ESTIMATION OF WHITE-TAILED DEER POPULATION SIZE

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Abstract: Estimation of population size is important for most research in population biology and in the management of game species. Using a stochastic, catch-effort, competing risks model (Dupont 1983), we estimated the population size of the Savannah River Site white-tailed deer (*Odocoileus virginianus*) herd for 1965–86. Population size varied markedly in response to changes in both hunting method and pressure. Still hunters preferentially harvested older animals compared to dog hunters. Deer were 2.37 times more susceptible to harvest from dog hunting than from still hunting. Hunter-induced mortality was estimated as 1.73 and 4.10 times as large as nonhunting mortality for still and dog hunting, respectively. The temporal pattern of estimated prehunt population sizes was significantly correlated with the temporal pattern of car–deer accidents recorded on the site during the same time period, suggesting that the temporal pattern of the population estimates is accurate. If the number of cohorts is large and an accurate estimate of hunter effort can be obtained, this technique may provide more reliable population estimates than previously available techniques because it imposes fewer and less stringent biological assumptions.

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Estimation of population numbers and density is a critical aspect of almost all studies in population ecology, population genetics, and wildlife management. Knowledge of population size is critical for an understanding of parameters such as mortality, natality (White et al. 1982), rate of increase or decrease (Caughley 1977), fitness (Manly 1985), effective population size (Crow and Kimura 1970, Shull and Tipton 1987), and processes such as competition (Murúa et al. 1987), dispersal (Gaines and Johnson 1987), selection (Manly 1985, Endler 1986), genetic drift (Crow and Kimura 1970, Kimura 1983), and gene flow (Endler 1977, Shields 1987). Additionally, if a population is subject to management, for either harvest or protection, a reliable estimate of population size is desirable.

Unfortunately, due to limitations imposed by underlying assumptions and/or the amount and kind of data required, estimating population size is rarely an easy or straightforward task (Burnham et al. 1980, Lefebvre et al. 1982, Seber 1982, White et al. 1982, Wilson and Anderson 1985).

Most recent work on population estimation techniques has involved either mark-recapture or line transect analyses. Large ungulates living in structurally complex habitats are virtually impossible to census directly and thus may not be amenable to the above techniques for population estimation (but see Kufeld et al. 1987), especially if population estimates are required over an extended time period. Track counts (McCaffery 1976) and pellet group counts

(Stormer et al. 1977) can provide an index of population size, but these methods can yield biased results that are sensitive to habitat differences. However, when used at a single location these relative indices can provide information for monitoring a population over time. Change-in-ratio methods (Conner et al. 1986) may be appropriate in structurally complex habitats; however, when the sex ratio of the sample approaches 1:1 this method is not effective (Conner et al. 1986). Therefore, in forested habitats, catch-effort or cohort methods may provide the only reliable population estimates for large ungulates. Most catch-effort methods require strong assumptions about the functional form of birth–death processes (Seber 1982) and require reliable estimates of hunter effort. Cohort methodologies (Pope 1972, Doubleday 1976) are stringent in their assumptions about natural mortality rates but do not require estimates of hunter effort. The available methodology usually imposes assumptions that cannot be justified in natural poulations due either to the natural history of the organism or the sampling regime employed (see review in Seber 1982).

Recently, Dupont (1983) used a stochastic catch-effort competing risks model of natural and hunter-induced mortality to develop a population estimation method. This method allows population size to be estimated from catch-effort data with fewer assumptions.

Our purpose was to use Dupont's method to estimate the numbers of individuals and the temporal patterning of population size for the Savannah River Site deer herd from 1965 to 1986. Additionally, we assessed the importance of annual hunts and hunting methods to population size dynamics.

MATERIALS AND METHODS
The Model

We assume a hazard regression model for deer mortality attributable to hunting and all other causes. This model is defined in terms of competing hazard functions:

$$\lambda_i(t) = \lambda l_i(t)\exp\left[\sum_{a=1}^{k} z_{1a}(t, i)\beta_a\right] \qquad (1)$$

$$\mu_i(t) = \mu m_i(t)\exp\left[\sum_{a=1}^{k} z_{2a}(t, i)\beta_a\right] \cdot \qquad (2)$$

where $\lambda_i(t)$ and $\mu_i(t)$ are the hunting and natural hazard functions, respectively, for deer from the ith cohort at time t_i. Lambda, μ, and (β_1, β_2, ..., β_k) are unknown model parameters and $l_i(t)$, $m_i(t)$, [$z_{1a}(t, i)$: $a = 1, \ldots, k$], and [$z_{2a}(t, i)$: $a = 1, \ldots, k$] are known covariate functions of time t and cohort i. The natural hazard function includes all sources of mortality other than direct hunting mortality. This includes death from wounding, death of fawns because their mother was shot, and all other human-induced mortality other than hunting, as well as natural mortality. The hazard functions $\lambda_i(t)$ and $\mu_i(t)$ are equal to the instantaneous risks of death due to hunting or all other causes, respectively, for an individual in the ith cohort at time t. Usually, $l_i(t) = l(t)$ is the hunter effort known to have been exerted at time t; $m_i(t)$ and [$z_{ja}(t, i)$: $j = 1, 2; a = 1, \ldots, k$] are optional functions that may be defined in any biologically realistic way in terms of factors known to affect deer mortality. Typically, the $z_{1a}(t, i)$ covariate functions are used to model age-specific hunter selectivity whereas the $m_i(t)$ and $z_{2a}(t, i)$ functions are used to model age-specific mortality due to all causes other than direct hunting mortality. Dupont (1983) illustrates how this can be done with indicator step functions z_{1a} and z_{2a}. The parameter μ may be replaced by a constant determined from other sources or analyses. The number of β parameters is optional and is denoted by k. When $k = 0$ and $m_i(t) = 1$, the model simplifies to:

$$\lambda_i(t) = \lambda l_i(t) \qquad (3)$$
$$\mu_i(t) = \mu. \qquad (4)$$

An iterative procedure is used to derive maximum likelihood estimates of the model parameters that are then used to produce population estimates. This model also employs a multinomial sampling distribution that can accommo-

date the large stochastic factors that affect the demography, genetics, and life history of natural populations. Standard errors of population estimates, χ^2 goodness-of-fit statistics, and cohort specific survivorship values are also provided.

The data required for this method are the cohort specific hunter kills in consecutive hunting intervals, the hunting effort required to obtain these kills, and any other information, such as sex, age, mass, etc., needed to define the optional covariate functions of the model. The optional covariate functions allow the incorporation of known differences in demographic response of sex, age, mass, etc. classes. Additionally, the user must supply some model of both the hunting and nonhunting hazard functions. The method is data intensive, both in terms of numbers of individuals and number of cohorts. The estimates derived by this method are dependent on 2 explicit assumptions. First, $\lambda_i(t)$ and $\mu_i(t)$ are correctly modeled by the hazard regression equations (1) and (2). An implicit assumption of equations (1) and (2) is that hunting and nonhunting mortality are additive and not compensatory. Second, the probability of >1 animal dying in a given short time interval is small compared to the probability of a single capture or death. This latter assumption has a critical effect on the method's standard error estimates and goodness-of-fit statistics. Violation of this last assumption will be discussed later. Additional model details are given in Dupont (1983).

The Database

Hunting Method.—The white-tailed deer population on the Savannah River Site (80,972 ha in Aiken, Barnwell, and Allendale counties, S.C.) has been subject to an annual harvest since 1965 and has been intensively studied since 1974 (Urbston 1976, Scribner et al. 1985). The site is divided into 50 hunt compartments for which 2 different hunt methodologies have been employed. Dog hunting was used in most compartments from 1965 through 1986. From 1969 through 1980 certain compartments were subjected to only still hunting. A detailed description of these differing hunting techniques and the study area can be found in Scribner et al. (1985). The hunting season for most years began in early October and ended in late December. Because only 2 or 3 compartments were hunted during any 1 day, the year was broken into 3 (dog hunted) or 2 (still hunted) time periods as

follows: nonhunting period (Jan 1–Sep 30), early dog hunt (Oct 1–Nov 15), late dog hunt (Nov 16–Dec 31), and still hunt (Oct 1–Dec 31). The number of hunting periods the database is divided into becomes an optimization process. Increasing the number of periods generally increases the accuracy of parameter estimates, however the periods need sufficient sample sizes of deer within periods and spatial sampling consistency among periods. Thus, we could not use individual hunt days as hunt periods. The temporal patterning of still hunts resulted in few deer being collected in the early hunt time period thus negating its usefulness.

Hunter Effort.—Hunter effort, the number of deer killed, and the number of car–deer accidents can be estimated with a fair degree of precision because of the limited public access to the Savannah River Site. Hunters are transported to and from their hunting sites at specified times, thus the number of man-days of effort can be accurately calculated. Hunter effort was estimated separately for dog-hunted and still-hunted areas because of differences in relative hunter success rates (0.111 and 0.288 for still-hunted and dog-hunted areas, respectively). Given these differences, the hunting hazard function is expected, a priori, to differ significantly between the 2 hunting techniques. Because our final estimates in the figures represent combined site-wide estimates, hunter effort was scaled, for presentation, by the yearly relative success of dog and still hunting techniques. The number of car–deer accidents represents those accidents reported to the site traffic division and thus may be a minimum number.

Animal Information.—All animals collected were weighed to the nearest pound, sexed, and aged by tooth eruption and wear (Severinghaus 1949). The data set contained 18,296 deer killed by hunters with dogs in 18 full of 29 total cohorts and 5,253 deer killed by hunters while still hunting in 14 full of 25 total cohorts over a 22-year period. Full cohorts are cohorts for which data are available for animals aged 0.5 to the maximum age recorded for that cohort or at least 4.5 years of age.

Model Implementation

Nonhunting Mortality.—The first step in modeling these catch-effort data was to look for evidence of varying age-specific nonhunting mortality rates. This was done by setting $m_i(t)$ = 1, $z_{1a}(t, i) = 0$, and $[z_{2a}(t, i); a = 1, \ldots, k]$ to
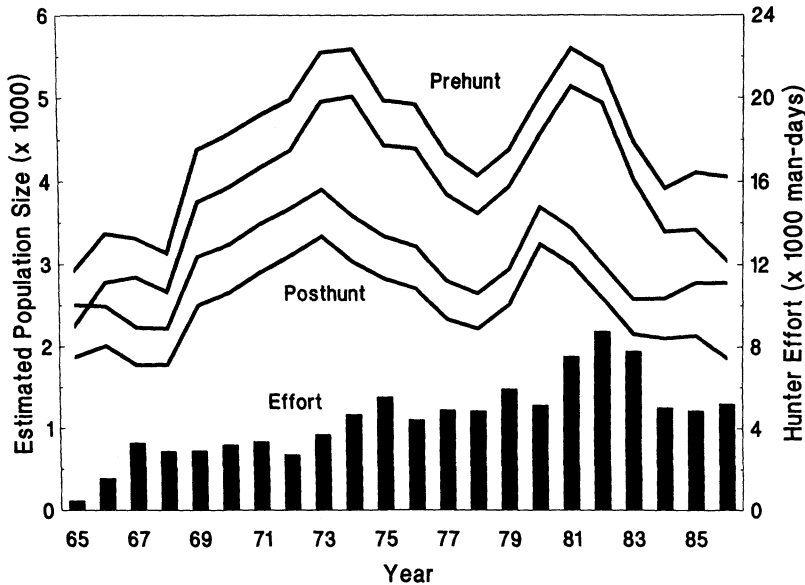
Fig. 1.   Ninety-five percent confidence limits of deer herd population sizes (combined still and dog hunts) for prehunt and posthunt populations from 1965 through 1986 on the Savannah River Site. Confidence limits were adjusted by using the square root of the mean-squared error as a variance inflation factor. Hunter effort for the same time period is expressed as the total number of both still and dog hunters weighted by the relative success rates, in that year, of the 2 techniques.

be indicator functions such that the nonhunting hazard for an a-year-old deer equals $\mu \exp(\beta_a)$. That is, $z_{2a}(t, i) = 1$ during the ath year of life of members of the ith cohort, and equals zero for all other values of t and i. These analyses were consistent with the hypothesis that nonhunting hazard does not vary with age and suggested the simple model defined by the hazard functions in equations (3) and (4). This latter model produced an estimate of $\mu = 0.30$ that corresponds to a 26% annual mortality rate. This value can be compared with the value calculated by Dapson et al. (1979) (38 vs. 26%) who used a different means and a more temporally restricted data set. We could not analyze year effects, and more importantly, age and year interactions because of small within cell sample sizes. Thus, we assumed that yearly changes in nonhunting mortality were not significant and were linearly related to age (i.e., no age and year interaction). We acknowledge that there might be significant age variation in nonhunting mortality, but without additional information, we chose the most parsimonious model that fit our data.

Age Variation.—We next investigated the effect of age on hunter selectivity. We fixed the value of μ at 0.30 and defined $[z_{1a}(t, i)]$ to be indicator functions such that the hunting hazard

for partially-recruited (i.e., "young") animals equaled $\lambda l(t)\exp(\beta_a)$, and the hunting hazard for fully recruited (i.e., "old") animals equaled $\lambda l(t)$. The β's were added as long as the model mean-squared error continued to decrease, and the model converged to a maximum likelihood solution. The final model for the dog-hunted areas contained selectivity parameters β_1 and β_2 for fawns (0.5 yr old) and yearlings (1.5 yr old), respectively. Similarly, selectivity parameters were used for fawns, yearlings, and 2.5-year-old deer in the still-hunted areas. Because we had no evidence of a consistent sex bias of adult animals in either the harvest or the herd (Scribner 1985) and because of sample size limitations, neither sex nor year effects were added to any of the models. More complex models, i.e., models containing additional β parameters, failed to converge to maximum likelihood parameter estimates. When goodness-of-fit statistics indicated a significant lack of fit, we used the variance inflation factor method described by Burnham et al. (1987:243–246) to adjust all variance terms. Thus, variances were multiplied by the model mean-squared error or standard deviations by the square root of mean-squared error.

Mantel Analysis.—We used Mantel matrix correlation analysis (Mantel 1967, Smouse et al. 1986) to examine the temporal patterning of the

Table 1.   Maximum likelihood estimates for model parameters and goodness-of-fit statistics for dog-hunted and still-hunted areas on the Savannah River Site, 1965–86.

Parameter	Dog-hunted		Still-hunted	
	Estimate	SD[a]	Estimate	SD[a]
Nonhunting mortality ($\hat{\mu}$)	0.30		0.30	
Hunting mortality ($\hat{\lambda}$)	1.23	0.109	0.52	0.078
Hunter selectivity				
0.5-yr-old deer ($\hat{\beta}_1$)	−0.87	0.079	−1.47	0.169
1.5-yr-old deer ($\hat{\beta}_2$)	−0.61	0.076	−1.04	0.180
2.5-yr-old deer ($\hat{\beta}_3$)			−0.44	0.187
χ^2	2,433.36		1,201.08	
MSE[b]	10.91		13.97	

[a] Standard deviations are corrected by multiplication with a variance inflation factor defined as the square root of the mean-squared error.
[b] Mean-squared error (MSE) = $\chi^2/$df.

poulation estimates. This is a matrix correlation analysis in which individual cells of the matrix are not correlated in a pairwise manner. Rather, the entire difference or distance matrix is correlated with another difference or distance matrix of identical rank. In essence the pattern of differences or distances in 1 matrix is compared with those in the second matrix. Significance of the correlation is obtained by comparing the observed R with those obtained through a series of permutational rearrangements of the original matrices. Statistical significance for a positive R is indicated by $P > 0.95$ and for negative R by $P < 0.05$.

The computer software was written in standard FORTRAN-77 and run on a VAX 11/750 computer. Copies of the source code containing the main programs, subroutines, and example hazard routines are available on magnetic tape from the third author.

RESULTS

Model Parameters.—Population size varied considerably between 1965 and 1986, with a difference between highest and lowest estimated values of 81% (2,001–3,621) posthunt and 107% (2,591–5,368) prehunt (Fig. 1). The absolute values of the estimated parameters are difficult to interpret because they are mathematical derivatives of the hazard functions (Table 1). However, the β's only affect animals that are not considered fully recruited into the huntable population. Therefore, the relative values of λ for adult deer show that they are 2.37 times as likely be killed by hunters on dog-hunted areas than on still-hunted areas. In addition a deer is 1.73 and 4.10 times as likely to die from direct hunter mortality than nonhunting mor-

tality on still- and dog-hunted areas, respectively. Two-way Mantel matrix correlation analysis yielded a significant correlation ($R = 0.90$, $P > 0.99$) between the temporal patterns of prehunt and posthunt population sizes. This result merely reiterates the relative difference between parameter estimates described earlier.

Model Fit.—Chi-square goodness-of-fit statistics and the mean-squared error indicated a lack of model fit for both the dog-hunted and still-hunted areas (Table 1). This is most likely due to a violation of the independence of fates assumption. However, indirect evidence of the accuracy of our estimates over time is provided by a significant correlation of the temporal pattern of prehunt population size estimates and the temporal pattern of car–deer accidents (Fig. 2) ($R = 0.52$, $P > 0.99$) using 2-way Mantel analysis.

Hunter Selectivity.—Selectivity parameters from the model, β, have been scaled to vary between 0 and 1 by presenting them in Figure 3 as $\exp^\beta$. The scaled parameters can then be viewed as representing the probability that a hunter when presented with a deer of that age class will shoot and kill the animal. Age selectivity is greater for still hunters (Fig. 3). This is indicated both by the still-hunting curve lying below the dog-hunting curve for deer aged <3.5 years and the ability to estimate 3 β's for the still hunting database and only 2 β's for the much larger dog hunting database (Table 1). Thus, still hunters preferentially take older age class animals compared to dog hunters.

DISCUSSION

Model Parameters.—Given the model assumption that hunting and nonhunting mortal-
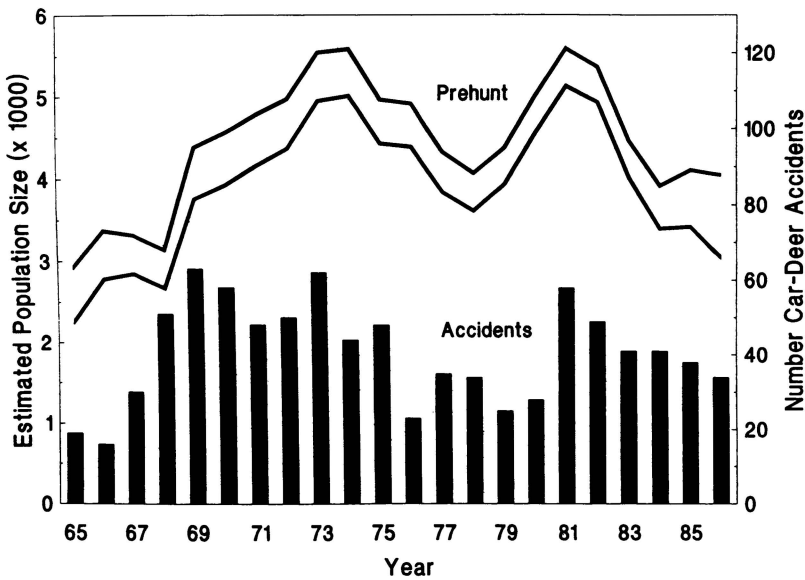
Fig. 2.   Number of car–deer accidents over time on the Savannah River Site. Prehunt population size estimates are also shown for comparison.

ity are additive and not compensatory effects, our results indicate that the size of the deer herd may be affected more by hunting than non-hunting mortality, and changes in demography and genetics are more likely to result from changes in hunting pressure than any other mortality factor. This inference is dependent on the assumption of additivity of mortality and among year stability in nonhunting mortality. The inference does agree with previous analyses that show hunting mode (dog vs. still) to be an important determinant of demographic and genetic structure (Scribner et al. 1985). However, our analysis shows that changes in population
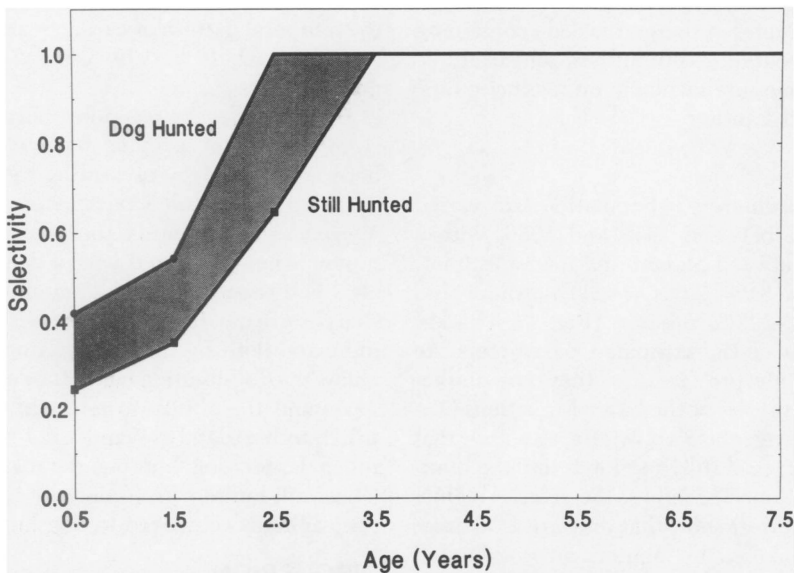

Fig. 3.   Age-related selectivity for dog- and still-hunted areas showing the estimated age-specific hunter hazard relative to that for fully-recruited (adult) animals. Selectivity is represented as $\exp^{\beta}$ so that it varies between zero (complete selectivity) and 1 (no selectivity). The shaded portion represents the difference in selectivity of dog and still hunters.

size were large during the time period used for the previous analysis (1977–82) by Scribner et al. (1985), and therefore, the main effect of hunting technique is confounded with changes in both actual and effective population size over that time period.

Model Fit.—Violation of the independence of fates assumption will cause a lack of model fit. Clearly, individual fates are not totally independent. For example, deer often travel in small groups (Ivey and Causey 1988), and young fawns are killed indirectly when their mothers are killed, thus inflating μ relative to λ. Lack of fit results from the inflated error variance and excess variation (Dupont 1983). Three additional factors may also contribute to the lack of fit. First, within the dog-hunted area, the compartments hunted may not be exactly the same for both the early and late hunting periods either within or among years. Second, for both the still- and dog-hunted areas, not all compartments within the area may be hunted every year, and the temporal sequence of hunting the compartments may also vary between years. Thus, the potential confounding of temporal and spatial variation may also inflate the variance estimates and lead to lack of fit of the model. Finally, we lack the sample sizes and a temporally appropriate sampling scheme to make strong inferences about temporal changes in nonhunting mortality or about whether there is any compensation between hunting and nonhunting mortality. These sources of variation may affect the precision of the estimate in any 1 year, but should not significantly bias the estimates. Thus, the temporal patterning of population size estimates should be only minimally affected. This is shown by the Mantel analysis of estimated population size and the number of car–deer accidents. The size of the data set and the precision with which we can quantify both hunter effort and number of deer killed, due to the limited public access of the Savannah River Site, increases confidence of our estimates. In addition, the survivorship estimates from the model agree with recruitment data obtained from fetal counts (Rhodes et al. 1985).

Hunter Selectivity.—The difference in selectivity between dog- and still-hunters is an expected result of the different hunting techniques as well as the specific instructions given to hunters. Briefly, the dog hunters are instructed to shoot any deer that is driven by their stand and are discouraged from being selective (see Scrib-

ner et al. 1985). Smith et al. (1983) and Scribner et al. (1985) assumed that density dependent regulation of demographic and genetic processes was unimportant on the Savannah River Site if the population was well below carrying capacity (Johns et al. 1977) and that changes in hunting pressure were independent of population size changes. This analysis suggests that changes in hunting pressure are not independent of population size changes in this population. Our analysis, as well as previous analyses (Scribner et al. 1985) have shown, assuming an additive relationship between hunting and nonhunting mortality, that changes in hunting pressure can produce changes in population size. It follows that correlated responses in both demography and genetics are expected, regardless of the population's relation to environmental carrying capacity.

Management Implications

Usefulness of Dupont's (1983) technique to other investigators and managers will be determined by the characteristics of their data sets. Specifically, a large number of individuals and cohorts as well as accurate estimates of hunter effort, hunting mortality, and age will be required to successfully implement Dupont's technique. Check station data may be of sufficient quantity and quality to produce reliable estimates. An important consideration may be to minimize variation in aging among years by limiting the number of different people responsible for aging the animals. If population estimates are required for an area that is not hunted in its entirety every sampling period, then the time sequence for sampling different areas should be kept as constant as possible between years.

The relative freedom from assumptions, the ability to put confidence limits on population estimates, the freedom to define covariate functions to fit local demographic and environmental idiosyncrasies, and the relative ease of data collection make Dupont's method a potentially useful technique for wildlife managers, especially in areas where game populations are subject to a heavy harvest and where other techniques are either inappropriate or too costly.

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