Electrophoretic Comparison of Road-killed Deer and Live-captured Deer Sampled by Muscle Biopsy

Mary J. Ratnaswamy, *Daniel B. Warnell School of Forest Resources, University of Georgia, Athens, GA 30602*

Carolyn L. Rogers, *Daniel B. Warnell School of Forest Resources, University of Georgia, Athens, GA 30602*

Robert J. Warren, *Daniel B. Warnell School of Forest Resources, University of Georgia, Athens, GA 30602*

Michael H. Smith, *Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29802 and Departments of Genetics and Zoology, Institute of Ecology, Daniel B. Warnell School of Forest Resources, University of Georgia, Athens, GA 30602*

Karl A. K. Stromayer, *Daniel B. Warnell School of Forest Resources, University of Georgia, Athens, GA 30602*

Abstract: A safe and effective muscle biopsy procedure that can be used to sample genetic variation in live white-tailed deer (*Odocoileus virginianus*) is described. The validity of this procedure for estimating genetic variability was confirmed by sampling blood and muscle from 78 road-killed and 57 captured deer at Chickamauga Battlefield National Military Park, Georgia, between June 1991 and June 1992. Six polymorphic loci were detected in muscle tissue and 2 polymorphic loci were found in blood using starch-gel electrophoresis. We compared levels of genetic variation in 3 sampling groups: road-killed deer, "actively" captured deer, and "passively" captured deer. Deer were considered "active" captures if the capture method did not involve baiting at the capture site (i.e., drive-nets, poaching, scientific collections, remote darting). Deer were classified as "passive" captures if bait was used to attract deer to the capture location (e.g., drop-nets, corral-drive nets, remote darting over bait). No significant differences were found between road-killed and captured deer for mean heterozygosity, mean number of alleles, or average allele frequencies.

Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 47:211–221

White-tailed deer are among the most genetically variable mammals (Smith et al. 1978). Many studies have examined the spatial and temporal heterogeneity of genetic variation in this species (Ramsey et al. 1979, Sheffield et al. 1985, Kennedy

et al. 1987) as well as the loss of heterozygosity after population bottlenecks (Hillestad 1984). Managers can use genetic information to identify "management units" (Manlove et al. 1976) and to design appropriate strategies for maximizing genetic diversity (Frankel 1983) and productivity of deer populations (Smith et al. 1982, Cothran et al. 1983, Chesser and Smith 1987).

Most studies evaluating genetic characteristics of deer populations have obtained post-mortem tissue samples by sampling hunter-harvested animals (Chesser et al. 1982, Sheffield et al. 1985, Karlin et al. 1989). In this paper, we describe a safe and effective procedure to sample genetic variation in live white-tailed deer by taking a muscle biopsy. We also compare levels of genetic variation observed in 3 sampling groups: 1.) road-killed deer; 2.) "actively" captured deer that were obtained without baiting (e.g., shot or aggressively driven into nets); and 3.) "passively" captured deer that came voluntarily to a baited capture site (e.g., drop-netted).

We hypothesized that genetically-based behavioral differences might predispose certain individuals more likely to be killed on roads or captured by active vs. passive means, which would be evidenced by significant genetic differences between these sampling groups. Previous studies have documented a correlation between genetic characteristics and behavioral traits such as aggression and exploratory behavior (Garten 1976, 1977), social dominance (Baker and Fox 1978), dispersal (Krebs and Meyers 1974), and survivorship (Chesser et al. 1982).

We hypothesized that passively captured deer would have lower levels of genetic variability (e.g., allele diversity) than road-killed or actively captured deer. This result would be anticipated if related deer (family groups) were most likely to forage together, thus increasing our likelihood of capturing related animals by passive methods. Female philopatry has been documented in white-tailed deer (Mathews 1989, Porter et al. 1991). The selective sampling of related animals probably would not provide as much genetic variation as more random sampling across the total population (e.g., road-kills). We discuss implications of our results for wildlife management and conservation of genetic resources.

We are grateful to C. Crumbley and numerous National Park Service (NPS) personnel for assistance with all aspects of sample collection. Additional help was provided by many volunteers, including local citizens and students from the University of Georgia. We thank P. E. Johns and J. L. Boone for technical advice in the laboratory, and O. E. Rhodes, Jr. for helpful suggestions on statistical analysis. Sample collection was funded by NPS Subagreement No. CA-5000-1-9017/8 and MacIntire-Stennis Project No. GEO-0030. Laboratory facilities and support were provided by a contract (DE-AC09-76SR00-819) between the U.S. Department of Energy and the Savannah River Ecology Laboratory of the University of Georgia.

Methods

Study Area

Chickamauga Battlefield National Military Park was established in 1890 in northwestern Georgia to preserve an important Civil War battle site. The NPS

manages the cultural and natural resources of the Park to preserve and protect the historic scene of that event in 1863. Chickamauga Battlefield consists of 1,987 ha of mixed hardwood (primarily *Quercus* and *Carya* spp.) and conifer (*Juniperus virginiana, Pinus* spp.) forests, 223 ha of mowed fields, 8 ha of cedar glades, and 20 ha of roadside habitat and buildings (Rogers et al. 1993*a*). Chickamauga Creek forms the southeastern boundary of the Park.

Regulated hunting is not permitted within the Park. Three 2-lane county roads traverse the Park and carry a substantial amount of commuter, commercial, and visitor traffic. The combination of favorable deer habitat (Harlow 1984) within the Park (e.g., bottomland hardwoods, fields, wood-field edges), adjacent agricultural areas, and high-volume vehicular traffic has led to more than 100 deer-vehicle collisions at the Park annually (Rogers et al. 1993*b*).

Collection of Samples from Road-killed Deer

Between June 1991 and June 1992, 78 road-killed deer (33M:45F) were collected from all sections of the Park or from within 1 km of Park boundaries. Each road-killed deer was sexed and uniquely identified. Age was estimated by tooth eruption and wear (Severinghaus 1949). Moore and Yates (1983) indicated that mammalian tissue samples collected within 12 hours of death (e.g., heart, liver, kidney) are suitable for electrophoretic analysis. Heart puncture was generally employed to collect whole blood (10 cc) into non-heparinized blood tubes. Blood was not drawn from deer that were dead more than 12 hours (as indicated by severe bloating). Blood samples were stored on wet ice until refrigerated and centrifuged (high speed for 10 minutes) within 2 days of collection. Plasma and hemolysate were pipetted into separate 2-ml cryogenic vials and placed in liquid nitrogen. Muscle samples (2 g) were dissected from the carcass using a knife, placed in 2-ml cryogenic vials, and stored on wet ice until placed in liquid nitrogen. Tissue samples were stored in liquid nitrogen (-90° C) or an ultracold freezer (-60° C) until electrophoretic analysis was performed.

Collection of Samples from Captured Deer

Fifty-seven deer (19M:38F) were captured from all sections of the Park between June 1991 and June 1992. Active capture methods included herd health collections ($N = 10$), poaching ($N = 6$), remote darting ($N = 5$), and drive-netting ($N = 2$). Poached animals were killed by unknown persons, but found by research or NPS personnel. Deer collected for herd health evaluations were killed by research personnel. Passive capture methods involved drop-nets ($N = 24$), corral-drive nets ($N = 9$), and remote darting over bait ($N = 1$). Drop-nets (Silvy et al. 1990) and corral-drive nets (Warren and Ford 1989) were pre-baited with a mixture of whole corn and "sweet feed" (grain and molasses) for a period of at least 1 to 4 weeks before capture efforts were initiated.

Poached and scientifically collected deer were sampled similarly to road-killed deer. Darted and netted deer were immobilized using a 1:6 mixture of xylazine hydrochloride (Rompun™, 100 mg/ml) and ketamine hydrochloride (Ketaset™,

100 mg/ml) as described by Mech et al. (1985). The risk of capture myopathy was reduced by keeping noise to a minimum around immobilized animals, keeping blindfolds on deer during the entire time of capture, and administering intraperitoneally at least 250 cc of a 1,000 mEq sodium bicarbonate-saline infusion (Mech et al. 1985, Conner et al. 1987).

A unique identification number, sex, age-class (fawn/yearling/adult), and estimated age were recorded. Forty of the live-captured deer were affixed with radio-collars that included a mortality mode sensor. Blood (10 cc) was collected from live deer at the jugular vein and placed into non-heparinized blood tubes. Muscle samples (1 g) were collected from live deer using a muscle biopsy procedure described below. Blood and muscle samples were processed as explained for road-killed deer. The effects of the immobilizing drugs were reversed within 40 minutes using an injection of a 10 mg/ml solution of yohimbine hydrochloride (Mech et al. 1985). Fawns were given 1 cc intravenously (IV) and 1 cc intramuscularly (IM). Adult does were administered 1.2 cc IV and 1.2 cc IM, while adult bucks received 1.5 cc IV and 1.5 cc IM.

Muscle Biopsy Procedure

Muscle samples were obtained from live deer as follows:

1) a battery-operated hair clipper (Oster Company, Milwaukee, Wis.) was used to shave a 10-cm by 10-cm area on the right rear flank over the *biceps femoris* muscle;

2) a total of 1 cc of lidocaine (20mg/ml) was injected (IM) at 4 places within the shaved biopsy site (but not directly into the incision) using a sterile 3-cc syringe and 18-ga (3.75 cm) needle;

3) cotton balls soaked with a dilute (80%) Betadine™ solution were used to swab the biopsy site in concentric circles, starting at the center of the biopsy site;

4) alcohol-soaked cotton balls were used to further clean the biopsy site and to remove the caustic Betadine™ solution, swabbing in concentric circles as described above;

5) Betadine™ and alcohol cleansings were repeated twice more;

6) a sterile scalpel blade (No. 21) was used to make a cross-shaped incision (6 mm long) through the skin at the center of the sterilized biopsy site;

7) after sliding the skin to the side to expose the surface of the muscle, a sterile 6-mm biopsy punch (Baker-Cummins Pharmaceuticals, Inc., Miami, Fla.; Order No. 0889) was then pressed firmly into the muscle to extract a small (about 0.2 g) sample of tissue;

8) sterile dissecting forceps were used to remove the muscle sample from the biopsy punch;

9) an additional muscle sample was obtained from each animal by gently sliding the skin to 1 side or another to expose a new section of muscle;

10) 1 cc of antibiotic (LA200: 200mg/ml oxytetracycline) was injected (IM) at the edge of the biopsy site using a sterile 3-cc syringe and 18-ga (3.75 cm) needle;

11) Topazone™ (Nitrofurazidone) antibiotic spray was applied to the entire shaved biopsy site;

12) the incision site was left unsutured.

Genetic Analysis

Blood and muscle samples were examined at 19 presumptive loci using horizontal starch gel electrophoresis (Selander et al. 1971, Manlove et al. 1975). Adenosine deaminase (Ada; E.C.3.5.4.4) was analyzed from muscle tissue on a lithium hydroxide gel. Isocitrate dehydrogenase (Icd-1, Icd-2; E.C.1.1.1.42) was scored from muscle on a tris-maleate gel. The remaining 16 enzymes were analyzed as described by Breshears et al. (1988): fumarate hydratase (Fh; E.C.4.2.1.2), mannosephosphate isomerase (Mpi-1; E.C.5.3.1.8), peptidase (Pep-1, Pep-2, Pep-3; E.C.3.4.11 or 3.4.13), creatine kinase (Ck-2, Ck-4; E.C.2.7.3.2), glucokinase (Gk), malic enzyme (Mod-1, Mod-2; E.C.1.1.1.40), and alpha-glycerophosphate dehydrogenase (aGpd-2) from muscle; albumin (Alb), plasma protein B (Ppt-B) and transferrin (Tf) from plasma; and 6-phosphogluconate dehydrogenase (6-Pgd; E.C.1.1.1.44) and b-hemoglobin (bHb) from hemolysate.

The program Biosys-1 (Swofford and Selander 1981) was used to compute allele frequencies, single-locus heterozygosity (h), mean multilocus heterozygosity (H), percentage of polymorphic loci (P), and the mean number of alleles per locus (A) for each sampling group. A locus was considered polymorphic if the frequency of the most common allele (i.e., mobility = 100) did not exceed 0.99. A chi-square test was used to test whether allele frequencies deviated from Hardy-Weinberg proportions. Levene's (1949) correction for small samples sizes was incorporated into all chi-square tests. At Hardy-Weinberg equilibrium, the proportion of homozygotes and heterozygotes would be that expected under conditions of random mating (panmictic breeding).

Wright's (1978) "*F*-statistics" were calculated using the Biosys-1 program. These statistics (F_{is}, F_{it}, F_{st}) were used to test whether the genetic variation found in the "total population" (all deer combined) was partitioned differently between road-kills, active captures, and passive captures (defined as "subpopulations" for this analysis). F_{is} is the deviation from Hardy-Weinberg proportions within subpopulations relative to the total population; F_{it} is the deviation from Hardy-Weinberg proportions in the total population; and F_{st} represents the level of genetic differentiation between subpopulations based on differences in allele frequency. Negative values of F_{is} and F_{it} indicate an excess of heterozygotes compared to the number of heterozygotes expected under Hardy-Weinberg equilibrium.

Road-killed deer were compared to active and passive captures separately, then to all captures combined. F_{st} values at each polymorphic locus were tested for significance using chi-square tests. Chi-square was calculated as $2NF_{st}$ (k - 1) with (k - 1) (s - 1) degrees of freedom, where N = total sample size, k = the number of alleles at that locus, and s = the number of subpopulations (Workman and Niswander 1970). Mean F_{st}, F_{is}, and F_{it} values were tested using a chi-square derived

by summing the chi-square values and degrees of freedom estimated at each locus. Statistical significance was defined at $P \leq 0.05$.

Results

Observations of 40 radio-collared deer indicated that muscle biopsy procedures had no apparent negative side-effects or secondary mortality, even after a period of several months. Two ear-tagged individuals that were visually observed within 2 weeks of the biopsy procedure exhibited no signs of infection at the biopsy site. Three live-trapped deer were subsequently killed by vehicles from 3 weeks to 5 months after undergoing the biopsy procedure. Examination of their biopsy sites revealed no signs of infection or tissue damage. Muscle tissue appeared normal and the skin had healed at the biopsy site. Mean age was not significantly different between road-killed deer (1.5 years, SE = 0.14, $N = 60$), active captures (2.3 years, SE = 0.29, $N = 23$), passive captures (1.5 years, SE = 0.19, $N = 34$), and all captures combined (1.9 years, SE = 0.17, $N = 57$).

Allele frequencies, single locus heterozygosities, and mean multilocus heterozygosities based on blood and muscle samples collected from road-killed and captured deer are presented in Table 1. Six of the 19 presumptive loci examined were polymorphic in all deer (Mpi-1, Ada, Mod-1, ∝Gpd-2, Tf, and βHb). Two additional loci (Pep-3 and Ck-2) were polymorphic only in passive captures (Table 1). Only Mod-2 for active captures ($P = 0.036$) and ∝Gpd-2 for passive captures ($P = 0.022$) were not in Hardy-Weinberg equilibrium. These deviations were probably because of chance effects related to sample size.

Mean number of alleles was not significantly different for road-killed deer (A = 1.58, SE = 0.21), active captures (A = 1.42, SE = 0.18), passive captures (A = 1.58, SE = 0.19), or all captures combined (A = 1.58, SE = 0.19). P was 31.58 for road-kills and active captures, and 42.11 for passive captures and all captures combined (0.95 criterion). H for all captures combined was 0.120 (SE = 0.049). H was not significantly different between any of the sampling groups (Table 1).

Wright's F-statistics for road-killed deer compared to active and passive captures separately demonstrated that the mean F_{st} was not significant (Table 2). However, allele frequencies were significantly different at 1 locus, βHB ($P < 0.025$). When road-killed deer were compared to all captures combined (Table 3), the mean F_{st} was not significant, but 1 locus (∝Gpd-2) was significantly different in allele frequencies ($P < 0.025$). Mean F_{st} and mean F_{it} values were not significant.

Discussion

Karesh et al. (1987) presented a remote method for collecting skin biopsy samples from free-ranging mammals. The biopsy procedure described here was used safely and effectively to collect muscle samples from live-captured white-tailed deer. We observed no long-term ill effects to deer as a result of our procedure, based on subsequent observations of radio-collared and ear-tagged individuals exposed to the natural conditions and stresses in the wild.

Table 1. Allele frequencies (Freq) at polymorphic loci, single-locus heterozygosity (h), and mean heterozygosity ($\bar{H}$) for road-killed, actively captured, and passively captured white-tailed deer collected at Chickamauga Battlefield, Georgia, 1991–1992.

		Road killed deer		Active captures		Passive captures	
Locus[a]	Allele	Freq	h[b]	Freq	h[b]	Freq	h[b]
Mpi-1	(*N*)	(78)		(22)		(32)	
	122	0.346	0.487	0.318	0.364	0.266	0.469
	100	0.654		0.682		0.734	
Pep-3	(*N*)	(68)		(22)		(28)	
	105	0.007	0.015	0.000	0.000	0.018	0.036
	100	0.993		1.000		0.982	
Ada	(*N*)	(78)		(22)		(32)	
	107	0.090	0.167	0.068	0.136	0.063	0.156
	100	0.904		0.932		0.922	
	95	0.006		0.000		0.016	
Ck-2	(*N*)	(32)		(13)		(23)	
	117	0.000	0.000	0.000	0.000	0.022	0.043
	100	1.000		1.000		0.978	
Mod-1	(*N*)	(70)		(22)		(29)	
	128	0.257	0.314	0.318	0.636	0.224	0.310
	100	0.743		0.682		0.776	
αGpd-2	(N)	(75)		(22)		(32)	
	112	0.213	0.347	0.318	0.455	0.359	0.281
	100	0.787		0.682		0.641	
Tf	(*N*)	(49)		(18)		(26)	
	100	0.918	0.122	0.889	0.222	0.981	0.038
	92	0.071		0.111		0.019	
	84	0.010		0.000		0.000	
βHb	(*N*)	(48)		(18)		(27)	
	95	0.302	0.583	0.528	0.722	0.333	0.741
	100	0.490		0.333		0.500	
	110	0.146		0.111		0.093	
	120	0.063		0.028		0.074	
$\bar{H}$[bc]			0.107		0.133		0.109
SE			0.043		0.054		0.047

[a] Locus abbreviations in text.
[b] Heterozygosities are direct count estimates.
[c] Mean multilocus heterozygosity includes 11 monomorphic loci.

Tissue samples obtained by using our muscle biopsy procedure were suitable for electrophoretic analysis. Muscle samples contributed 6 of the 8 variable loci in this study. Blood samples provided only 2 variable loci. Our muscle biopsy procedure allowed us to significantly increase the amount of genetic information obtained from live animals. Road-killed deer also were suitable for genetic studies if specimens were obtained within a reasonable time frame (i.e., 12 hours) as suggested by Moore and Yates (1983).

We compared genetic variation in road-killed, actively captured, and passively captured deer to investigate whether the sampling method would introduce a bias into the estimate of genetic variability for the total population. For example, if passive captures were more closely related, this could have led to a different es-

Table 2. *F*-statistics for comparison of road-killed, actively captured, and passively captured white-tailed deer collected at Chickamauga Battlefield, Georgia, 1991–1992. Chi-square tests significance of F_{st}.

Locus[a]	F_{is}	F_{it}	F_{st}	χ^2	DF
Mpi-1	-0.034	-0.028	0.005	1.32	2
Pep-3	-0.015	-0.008	0.006	1.42	2
Ada	-0.025	-0.023	0.002	1.06	4
Ck-2	-0.022	-0.007	0.015	2.04	2
Mod-1	-0.084	-0.075	0.008	1.94	2
αGpd-2	0.120	0.136	0.018	4.64	2
Tf	0.009	0.031	0.022	8.18	4
βHb	-0.097	-0.068	0.026	14.51[b]	6
x	-0.028	-0.013	0.015	35.10	24

[a] Locus abbreviations defined in text.
[b] Significant at $P \leq 0.05$.

timate of genetic variation for this subpopulation. Based on average genetic characteristics (H, A, P) and average F_{st} values, no sampling bias was detected in this study.

It is unknown whether any of the 3 sampling groups were a random sample of the total population. O'Gara and Harris (1988) concluded that road-killed deer were not a random sample of the total population based on body condition data. The large number of road-kills obtained during this study ($N = 78$), however, may represent a random sample of deer from the Park. The estimated size of the deer population in the Park based on spotlight survey data is 400–500 animals (unpubl. data).

Table 3. *F*-statistics for comparison of road-killed and captured (active and passive captures combined) white-tailed deer collected at Chickamauga Battlefield, Georgia, 1991–1992. Chi-square tests significance of F_{st}.

Locus[a]	F_{is}	F_{it}	F_{st}	χ^2	DF
Mpi-1	-0.059	-0.055	0.004	1.06	1
Pep-3	-0.009	-0.009	0.000	0.00	1
Ada	-0.005	-0.003	0.002	1.06	2
Ck-2	-0.014	-0.007	0.007	0.95	1
Mod-1	0.008	0.008	0.000	0.00	1
αGpd-2	0.111	0.130	0.021	5.42[b]	1
Tf	0.087	0.089	0.002	0.74	2
βHb	-0.033	-0.027	0.007	3.91	3
x	0.005	0.012	0.007	13.13	12

[a] Locus abbreviations defined in text.
[b] Significant at $P \leq 0.05$.

Management and Research Implications

Our muscle biopsy procedure can be applied in the field with low expected mortality and minimal effects on behavior after a few days of recovery time. Small sample sizes ($N < 100$) are sufficient to gain an estimate of genetic variation in a population, if variable loci can be identified in the muscle or blood samples. Conservation biologists interested in genetic characteristics of threatened or protected species could possibly use this procedure to obtain samples in a nondestructive manner from other live-captured animals. We recommend that a licensed veterinarian be consulted before initiating a study involving this procedure.

Managers considering restocking or translocation projects might use this technique to sample heterozygosity and allele frequencies within the target herd or within the source population. Genetically distinct or unusually inbred populations can be identified before management plans are enacted. Future research comparing genetic variation in hunter-harvested and live-captured deer from the same population would further confirm the validity of the biopsy procedure for genetic analysis of deer.

Literature Cited

Baker, M. C. and S. F. Fox. 1978. Dominance, survival and enzyme polymorphism in dark-eyed Juncos, *Junco hyemalis*. Evolution 32:697–711.

Breshears, D. D., M. H. Smith, E. G. Cothran, and P. E. Johns. 1988. Genetic variability in white-tailed deer. Heredity 60:139–146.

Chesser, R. K. and M. H. Smith. 1987. Relationship of genetic variation to growth and reproduction in the white-tailed deer. Pages 168–177 *in* C. Wemmer, ed. Biology and management of the Cervidae. Res. Symp. Natl. Zool. Park (1982). Smithsonian Inst. Press, Washington, D.C.

———, ———, P. E. Johns, M. N. Manlove, D. O. Straney, and R. Baccus. 1982. Spatial, temporal, and age-dependent heterozygosity of beta-hemoglobin in white-tailed deer. J. Wildl. Manage. 46:983–990.

Conner, M. C., E. C. Soutiere, and R. A. Lancia. 1987. Drop-netting deer: costs and incidence of capture myopathy. Wildl. Soc. Bul. 15:434–438.

Cothran, E. G., R. K. Chesser, M. H. Smith, and P. E. Johns. 1983. Influences of genetic variability and maternal factors on fetal growth in white-tailed deer. Evolution 37:282–291.

Frankel, O. H. 1983. The place of management in conservation. Pages 1–14 *in* C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, eds. Genetics and conservation: a reference for managing wild animal and plant populations. Benjamin-Cummings Publ. Co., Inc., Menlo Park, Calif.

Garten, C. T., Jr. 1976. Relationships between aggressive behavior and genic heterozygosity in the oldfield mouse, *Peromyscus polionotus*. Evolution 30:59–72.

———. 1977. Relationships between exploratory behavior and genic heterozygosity in the oldfield mouse. Anim. Behav. 25:328–332.

Harlow, R. F. 1984. Habitat evaluation. Pages 601–628 *in* L. K. Halls, ed. White-tailed deer: ecology and management. Stackpole Books, Harrisburg, Pa.

Hillestad, H. O. 1984. Stocking and genetic variability of white-tailed deer in the southeastern United States. Ph.D. diss., Univ. Ga., Athens. 112pp.

Karesh, W. B., F. Smith, and H. Frazier-Taylor. 1987. A remote method for obtaining skin biopsy samples. Conserv. Biol. 1:261–262.

Karlin, A. A., G. A. Heidt, and D. W. Sugg. 1989. Genetic variation and heterozygosity in white–tailed deer in southern Arkansas. Am. Midl. Nat. 121:273–284.

Kennedy, P. K., M. L. Kennedy, and M. L. Beck. 1987. Genetic variability in white-tailed deer (*Odocoileus virginianus*) and its relationship to environmental parameters and herd origin (Cervidae). Genetica 74:189–201.

Krebs, C. J. and J. H. Meyers. 1974. Population cycles in small mammals. Adv. Ecol. Res. 8:267–399.

Levene, H. 1949. On a matching problem arising in genetics. Annu. Math. Stat. 20:91–94.

Manlove, M. N., J. C. Avise, H. O. Hillestad, P. R. Ramsey, M. H. Smith, and D. O. Straney. 1975. Starch gel electrophoresis for the study of population genetics in white-tailed deer. Proc. Annu. Conf. Southeast Assoc. Fish and Wildl. Agencies 29:392–403.

———, M. H. Smith, H. O. Hillestad, S. E. Fuller, P. E. Johns, and D. O. Straney. 1976. Genetic subdivision in a herd of white-tailed deer as demonstrated by spatial shifts in gene frequencies. Proc. Annu. Conf. Southeast Assoc. Fish and Wildl. Agencies 30:487–492.

Mathews, N. E. 1989. Social structure, genetic structure and anti-predator behavior of white-tailed deer in the Adirondacks. Ph.D. diss., State Univ. New York Col. Environ. Sci. and For., Syracuse. 171pp.

Mech, L. D., G. D. Del Giudice, P. D. Karns, and U. S. Seal. 1985. Yohimbine hydrochloride as an antagonist to xylazine hydrochloride-ketamine hydrochloride immobilization of white-tailed deer. J. Wildl. Dis. 21:405–410.

Moore, D. W. and T. L. Yates. 1983. Rate of protein inactivation in selected mammals following death. J. Wildl. Manage. 47:1166–1169.

O'Gara, B. W. and R. B. Harris. 1988. Age and condition of deer killed by predators and automobiles. J. Wildl. Manage. 52:316–320.

Porter, W. F., N. E. Mathews, H. B. Underwood, R. W. Sage, Jr., and D. F. Behrend. 1991. Social organization in deer: implications for localized management. Environ. Manage. 15:809–814.

Ramsey, P. R., J. C. Avise, M. H. Smith, and D. F. Urbston. 1979. Biochemical variation and genetic heterogeneity in South Carolina deer populations. J. Wildl. Manage. 43:136–142.

Rogers, C. L., M. J. Ratnaswamy, and R. J. Warren. 1993*a*. Vegetation communities of Chickamauga Battlefield National Military Park, Georgia. Natl. Park Serv., Southeast Region, Tech. Rep. NPS/SERCHCH/NRTR–93/11. 83pp.

———, K. A. K. Stromayer, R. J. Warren, C. L. Tucker, and M. J. Ratnaswamy. 1993*b*. Roadkills, capture success, and mortality of radio-collared deer at Chickamauga Battlefield Park. Proc. Annu. Meet. Southeast Deer Study Group 16:23–24 (Abstract).

Selander, R. K., M. H. Smith, S.Y. Yang, W. E. Johnson, and J. B. Gentry. 1971. IV. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). Studies in Genetics VI. Univ. Texas Publ. 7103:49–90.

Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. J. Wildl. Manage. 13:195–216.

Sheffield, S. R., R. P. Morgan II, G. A. Feldhamer, and D. M. Harman. 1985. Genetic variation in white-tailed deer (*Odocoileus virginianus*) populations in western Maryland. J. Mammal. 66:243–255.

Silvy, N. J., M. E. Morrow, E. Shanley, Jr., and R. D. Slack. 1990. An improved drop net for capturing wildlife. Proc. Annu. Conf. Southeast Assoc. Fish and Wildl. Agencies 44:374–378.

Smith, M. H., M. N. Manlove, and J. Joule. 1978. Spatial and temporal dynamics of the genetic organization of small mammal populations. Pages 99–113 *in* D. P. Snyder, ed. Populations of small mammals under natural conditions. Special Publ. No. 5. The Pymatunig Symp. in Ecol., Univ. Pittsburg, Pittsburg, Pa.

———, R. K. Chesser, E. G. Cothran, and P. E. Johns. 1982. Genetic variability and antler growth in a natural population of white-tailed deer. Pages 365–387 *in* R. D. Brown, ed. Antler development in Cervidae. Caesar Kleberg Wild. Res. Inst., Texas A&I Univ., Kingsville.

Swofford, D. L. and R. K. Selander. 1981. BIOSYS-1: A FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. J. Hered. 72:281–283.

Warren, R. J. and C. R. Ford. 1989. A new corral/drive-net trap for multiple deer capture. Proc. Annu. Meet. Southeast. Deer Study Group 12:17–18 (Abstract).

Workman, P. L. and J. D. Niswander. 1970. Population studies on southwestern Indian tribes. II. Local genetic differentiation in the Papago. Am. J. Human Genet. 22:24–49.

Wright, S. 1978. Evolution and the genetics of populations, Vol. 4. Variability within and among natural populations. Univ. Chicago Press, Chicago, Ill. 580pp.