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GENETIC AND DEMOGRAPHIC PATTERNS OF THE RACCOON (*PROCYON  
LOTOR*) ACROSS EXTENDED SPATIO-TEMPORAL SCALES

by

John R. Hisey

A Dissertation

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

Major: Biology

The University of Memphis

December 2012

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## DEDICATION

To Lauren and Nathaniel, who endured my absence and took on many of my responsibilities over several years to enable me to finish this work;

And

To my God, who removed obstacles, protected from danger, provided material needs, and gave peace of mind in times of turmoil.

## ACKNOWLEDGMENTS

I am grateful for the extensive guidance in many aspects of this study provided by my major professor, Dr. Michael L. Kennedy. M. L. Beck, R. K. Chesser, S. G. Mech, T. Nakazato, and B. A. Simco critically reviewed previous drafts of this manuscript, and J. Wang provided suggestions on the determination of genealogical relationships using the program, *COLONY*. Data analysis, fieldwork, and other support by T. A. Ladine, D. M. Wolcott, E. H. Vecchio, E. Chukwurah, B. D. Carver, R. A. Baldwin, D. Van Vickle, and many other students and staff members at The University of Memphis and Lee University assisted greatly in this investigation. Several contributors donated tissue samples from various sites across the United States and Canada. The staff of Génome Québec provided substantial aid in genotyping the raccoons. Partial funding was provided by The Appalachian College Association, Lee University, the American Museum of Natural History, the American Society of Mammalogists, The University of Memphis Department of Biological Sciences, The University of Memphis Ecological Research Center, and Sigma Xi. Also, I thank those who fulfilled some of my responsibilities as a member of a family, a university faculty, and a community so that I could complete this study.

## ABSTRACT

Hisey, John R. Ph.D. The University of Memphis. December 2012. Genetic and Demographic Patterns of the Raccoon (*Procyon lotor*) Across Extended Spatio-temporal Scales. Major Professor: Michael L. Kennedy, Ph.D.

Population features and genetic structure of raccoons (*Procyon lotor*) and many other solitary-mammalian species are relatively unknown. To better understand these characteristics in *P. lotor*, microsatellite data collected at local, area, and transcontinental scales and 14 years of local mark-recapture data were used to assess the temporal and spatial extent of philopatry, dispersal, formation of lineages, and genetic patterns associated with these factors. Specifically, I tested the following predictions for raccoons: (1) long-term residency is common; (2) patterns of genetic variation are associated with isolation by distance; (3) closely related animals remain spatially clustered.

Only 26 of 215 *P. lotor* were recaptured over 2-10 years to become long-term residents, and just 1 juvenile remained philopatric for more than 1 year. Lower proportions of juveniles than other ages and of males than females became long-term residents. Most long-term residencies were established during periodic 2-year peaks in precipitation. The prediction that long-term residents would be common was not supported, and the observed pattern of genetic variability would not facilitate lineage-structuring in the population.

Genetic differentiation between sites appeared to be increased through: (1) isolation by distance at local, area, and transcontinental scales; (2) females remaining on local sites; and (3) landscape barriers to movement that could also reduce the spread of diseases by raccoons. Evidence in 22 individuals suggested movement between sites 75-

1200 km apart. The prediction that patterns of genetic variation are associated with isolation by distance was supported.

The distance between full sibs in 71 pairs inferred by genotypes from microsatellites was <1 km for 46 pairs and >69 km for 5 pairs, with a mean of 7.0 km. Rarely, did sib groups shift locations together, comprise more than 3 individuals, or remain intact in the same vicinity for more than a year. The spatial dispersion among related raccoons was greater in males than in females, in older adults than in younger adults, and during dry years than during wet years. These patterns could speed the spread of key diseases but did not support the prediction that closely related raccoons would remain geographically clustered over multiple years.

## PREFACE

This dissertation is in the form of three separate papers: (I) An assessment of long-term residency and temporal composition in a population of raccoons (*Procyon lotor*); (II) Genetic structure in the raccoon (*Procyon lotor*) at local to transcontinental scales; (III) Spatio-temporal dispersion of kin groups of the raccoon (*Procyon lotor*). The first 2 of these papers are in the style of the *Journal of Mammalogy* and the third paper is in the style of *The Southwestern Naturalist*. These are the journals to which these papers have been or will be submitted for publication. Appendices in this dissertation provide supporting data for interested investigators. References in this dissertation to Hisey (2012) refer to the dissertation as a whole.



## TABLE OF CONTENTS

	PAGE
LIST OF TABLES	x
LIST OF FIGURES	xv
CHAPTER	
I. Introduction	1
II. An Assessment of Long-Term Residency and Temporal Composition in a Population of Raccoons ( <i>Procyon lotor</i> ).	7
Introduction	7
Materials and Methods	9
Results	12
Discussion	23
Conclusions	36
Acknowledgments	37
Literature Cited	38
III. Genetic Structure in the Raccoon ( <i>Procyon lotor</i> ) at Local to Transcontinental Scales.	44
Introduction	44
Materials and Methods	47
Results	53
Discussion	65
Conclusion	80
Acknowledgments	81
Literature Cited	82
IV. Spatio-temporal Dispersion of Kin Groups of the Raccoon ( <i>Procyon lotor</i> ).	89
Introduction	89
Materials and Methods	91
Results	96
Discussion	104
Conclusion	116
Acknowledgments	117
Literature Cited	118
V. Conclusion	127

## APPENDICES

Appendix I	129
Appendix II	133
Appendix III	137
Appendix IV	152

LIST OF TABLES

CHAPTER	PAGE
<p><b>I. An Assessment of Long-Term Residency and Temporal Composition in a Population of Raccoons (<i>Procyon lotor</i>).</b></p>	
<p><b>TABLE 1.</b>—Trends from 1992 to 2002 in long-term residency and turn-over rates of raccoons (<i>Procyon lotor</i>) from winter to winter and annual precipitation at the Meeman Biological Station (Meeman) in western Tennessee. Values in table are: 1. The number of individuals 1st captured each year on the Meeman grid; 2. The number of individuals 1st captured each year on the Meeman grid that became long-term residents by remaining on the grid over a total span of 3 breeding seasons (2 yr. minimum turn-over time); 3. The remainder of individuals 1st captured each year on the Meeman grid that disappeared from the grid before becoming long-term residents; 4. Percent of those individuals 1st captured each year on the Meeman grid that remained to become long-term residents; 5. Number of all individuals captured each winter from 1991 to 2003; 6. Number of all individuals captured each winter that were also captured the following year; 7. Number of all individuals captured each winter that were not captured the following year; 8. Percent of all individuals captured each winter that were also captured the following year; 9. Percent of all individuals captured each winter that were not captured the following year (annual turn-over rate); 10. Numbers of individuals of combined age classes 2 through 5 first appearing on the grid during a year; and 11. Annual cm of precipitation at Meeman. Each individual was considered as a separate independent trial.</p>	13
<p><b>TABLE 2.</b>—Trends in long-term residency of raccoons (<i>Procyon lotor</i>) by age class at the Meeman Biological Station in western Tennessee. Values in table are: numbers of all individuals captured from 1992 to 2002 that were of each age class at first capture (sample size); those first capture raccoons that became long-term residents (those captured on the grid over at least 24 months or 3 breeding seasons); those that were resident for less than 24 months (3 breeding seasons) and so did not become long-term residents; and percent of first captures becoming long-term residents. See text for explanation of age-class categories.</p>	16
<p><b>TABLE 3.</b>—Trends in long-term residency of raccoons (<i>Procyon lotor</i>) by sex at the Meeman Biological Station in western Tennessee. Values in table are: numbers of all individual raccoons of each sex first captured from 1992 to 2002 (sample size); those that became long-term residents (captured on the grid over at least 24 months or 3 breeding seasons); those that were resident for less than 24 months (3 breeding seasons) and so did not become long-term residents; and percent of first captures becoming long-term residents. See text for explanation of age-class categories.</p>	17

**TABLE 4.**—Comparison of rates of first appearance and last appearance (disappearance) among age and sex classifications for raccoons (*Procyon lotor*) at the Meeman Biological Station in western Tennessee. Of (n) individuals in each sex and age class captured during any winter 1991-2004, the proportion not captured the previous winter is the percent of first appearance and the proportion not captured the following winter is the percent of last appearance. The same individual could be present during more than 1 year in the same or different age class and was counted and used in the calculations again each additional year it was present. See text for explanation of age-class categories.

20

**TABLE 5.**—Individual turn-over times (span of years taken for an animal to disappear from the site) of raccoons (*Procyon lotor*) captured at the Meeman Biological Station in western Tennessee from 1991 to 2000: total numbers of each sex first captured in each age class (1-5); numbers that were recaptured at maximum terms of residency (individual turn-over times) of 0-10 years; and mean individual turn-over time in years (and standard error). See text for explanation of age-class categories.

21

## **II. Genetic Structure in the Raccoon (*Procyon lotor*) at Local to Transcontinental Scales.**

**TABLE 1.**—F-Statistics and number of migrants per generation (Nm) for raccoons (*Procyon lotor*) determined as part of a study of genetic structure of microsatellite loci at local to transcontinental scales across the United States and Canada. F-Statistics and Nm at each microsatellite locus are over all sites over all transcontinental regions (A), sites in the southeastern area (B), and local trapping grids at the Meeman Biological Station and the Ames Plantation in southwestern Tennessee (C). F-statistics and probability values for all populations and loci were also pooled for each of these data sets. *P* is the probability, based on permutation across the full data set, that the actual data set has lower values than randomly selected sets for  $F_{ST}$ ,  $F_{IS}$ , and  $F_{IT}$ .  $F_{ST}$  is the degree of genetic differentiation among the subpopulations within the population.  $F_{IS}$  and  $F_{IT}$  are, respectively, departure from expectations for random mating for individuals within a subpopulation and such a departure for all of the individuals for the entire population.

62

**TABLE 2.**—Pairwise degree of genetic differentiation between subpopulations within the overall population ( $F_{ST}$ ) for microsatellite loci of raccoons (*Procyon lotor*) determined as part of a study of genetic structure at local to transcontinental scales across the United States and Canada.  $F_{ST}$  values are given below the diagonals and probability values based on 999 permutations are given above the diagonals of the tables. The “\*” probability values were significantly different from 0 at  $P \leq 0.05$  after the

Bonferroni adjustment for Type 1 error for transcontinental regions (a), sites in the southeastern area (b), and local trapping grids at the Meeman Biological Station and the Ames Plantation in southwestern Tennessee (c). See text for abbreviations for the sites, and explanations.

63

## Appendix I

**TABLE 1.**—Turn-over rates (the percentage of all individuals captured on a site during a year that were not recaptured there the following year) of raccoons (*Procyon lotor*) by sex and age class at the Meeman Biological Station in western Tennessee. Values in table are: total numbers of individual raccoons in each sex and age class captured during any winter 1991-2003; numbers captured during a year that were recaptured the following year, numbers captured during a year that were not recaptured the following year, percent of individuals captured during a year that were recaptured the following year, and percent of individuals captured during a year that were not recaptured the following year (=annual turn-over rate). Each individual was considered as a separate independent trial. See text for explanation of age-class categories.

132

## Appendix III

**TABLE 1.**—Mean and standard error (SE) of observed and expected heterozygosity ( $H_o$  and  $H_e$ , respectively) for each population over the 8 microsatellite loci analyzed for n individual raccoons (*Procyon lotor*) that were sampled to determine genetic structuring at 3 scales across the United States and Canada. Scales included: a) transcontinental regions; the site of the population (Pop.) for NW (Northwest) included Oregon only; NMW (Northern Midwest) included Manitoba and Wisconsin; NE (Northeast) included New York and Vermont; EC (East Central) included Indiana, Kentucky, and Tennessee; SMW (Southern Midwest) included Texas, Louisiana, Arkansas, and Kansas; and SE (Southeast) included Alabama, Georgia, and South Carolina. b) Transcontinental states; the sites of the populations were identified by state and province abbreviations for Alabama, Arkansas, Georgia, Indiana, Kansas, Kentucky, Louisiana, Manitoba, New York-Vermont, Oregon, South Carolina, Tennessee, Texas, and Wisconsin, respectively. c) Southeastern area; the sites of the populations were, respectively, Arkansas, Georgia, Indiana, eastern Kentucky, western Kentucky, South Carolina, northeastern Tennessee, northwestern Tennessee, and southwestern Tennessee. d) Trapping grids in southwestern Tennessee. Identifiers were M for the Edward J. Meeman Biological Station; and for the Ames Plantation, AC, D, H, MC, and P were grids at Afternoon Course, Dusco Place, Hancock Place, Morning Course, and Pattersonville, respectively.

139

**TABLE 2.**—Mean and standard error (SE) of observed and expected heterozygosity ( $H_o$  and  $H_e$ , respectively) over the combined populations for each of the 8 microsatellite loci analyzed for raccoons (*Procyon lotor*) in a study of genetic structure at different geographic scales across the United States and Canada. a) and b): Data at the transcontinental scale analyzed by regions and states, respectively; c) Sites in the southeastern area; d) Trapping grids in southwestern Tennessee.

142

**TABLE 3.**— $P$ -value and standard error (SE) for the global test for the alternate hypothesis of heterozygote deficit across the combined 8 microsatellite loci analyzed for each population (Pop.) of raccoons (*Procyon lotor*) sampled in a study of genetic structure at different geographic scales across the United States and Canada. Scales included: a) Transcontinental regions; the site of the population (Pop.) at NW (Northwest) included Oregon only; NMW (Northern Midwest) included Manitoba and Wisconsin; NE (Northeast) included New York and Vermont; EC (East Central) included Indiana, Kentucky, and Tennessee; SMW (Southern Midwest) included Texas, Louisiana, Arkansas, and Kansas; and SE (Southeast) included Alabama, Georgia, and South Carolina. b) Southeastern area; the sites of the populations were, respectively, Arkansas, Georgia, Indiana, eastern Kentucky, western Kentucky, South Carolina, northeastern Tennessee, northwestern Tennessee, and southwestern Tennessee. c) Trapping grids in southwestern Tennessee. Identifiers were M for the Edward J. Meeman Biological Station; and for the Ames Plantation, AC, D, H, MC, and P were grids at Afternoon Course, Dusco Place, Hancock Place, Morning Course, and Pattersonville, respectively. “\*”  $P$ -values indicate sites with significant ( $P \leq 0.05$ ) heterozygote deficits with 8 loci included after the Bonferroni adjustment for Type 1 error.

143

**TABLE 4.**— $P$ -value and standard error (SE) for the global test for the alternate hypothesis of heterozygote deficit for each of 8 microsatellite loci analyzed across combined populations of raccoons (*Procyon lotor*) sampled in a study of genetic structure at different geographic scales across the United States and Canada. a) Transcontinental populations including Alabama, Arkansas, Georgia, Indiana, Kansas, Kentucky, Louisiana, Manitoba, New York, Oregon, South Carolina, Tennessee, Texas, Vermont, and Wisconsin. b) Populations in the southeastern area comprising Arkansas, Georgia, Indiana, eastern Kentucky, western Kentucky, South Carolina, northeastern Tennessee, northwestern Tennessee, and southwestern Tennessee. c) Populations in southwestern Tennessee comprising trapping grids at the Edward J. Meeman Biological Station; and the grids at the Ames Plantation at Afternoon Course, Dusco Place, Hancock Place, Morning Course, and Pattersonville. The “\*”  $P$ -values indicate loci with significant ( $P \leq 0.05$ ) heterozygote deficits with all combined sites included, after the Bonferroni adjustment for Type 1 error.

144

**TABLE 5.**—Matrix of relationships between pairs of populations, based on 8 microsatellite loci for raccoons (*Procyon lotor*) sampled in a study of genetic structure at different geographic scales across the United States and Canada. Numbers of migrants per generation ( $N_m$ ) are above the diagonal and Nei (1987) standard genetic distances ( $D_s$ ) below the diagonal. a) Transcontinental regions; for identifiers, NW (Northwest) included Oregon only; NMW (Northern Midwest) included Manitoba and Wisconsin; NE (Northeast) included New York and Vermont; EC (East Central) included Indiana, Kentucky, and Tennessee; SMW (Southern Midwest) included Texas, Louisiana, Arkansas, and Kansas; and SE (Southeast) included Alabama, Georgia, and South Carolina. b) Transcontinental states; population identifiers were state and province abbreviations for Alabama, Arkansas, Georgia, Indiana, Kansas, Kentucky, Louisiana, Manitoba, New York-Vermont, Oregon, South Carolina, Tennessee, Texas, and Wisconsin, respectively. c) Sites in the southeastern area; population identifiers were, respectively, Arkansas, Georgia, Indiana, eastern Kentucky, western Kentucky, South Carolina, northeastern Tennessee, northwestern Tennessee, and southwestern Tennessee. d) Grids in southwestern Tennessee; identifiers were M for the Edward J. Meeman Biological Station; and for the grids at the Ames Plantation, were AC, D, H, MC, and P for Afternoon Course, Dusco Place, Hancock Place, Morning Course, and Pattersonville, respectively.

145

#### Appendix IV

**TABLE 1.**—Locations, identification numbers, and genotypes at 9 microsatellite loci for 655 raccoons (*Procyon lotor*) used in analyses of genetic structure at 3 geographic scales across the United States and Canada: transcontinental, southeastern area, and local southwestern Tennessee sites. Site abbreviations are for Alabama (AL), Arkansas (AR), Georgia (GA), Indiana (IN), Kansas (KS), Kentucky (KY), eastern Kentucky (KYE), western Kentucky (KYW), all other Kentucky locations (KY), Louisiana (LA), Manitoba (MB), New York-Vermont (NYVT), Oregon (OR), South Carolina (SC); northeastern Tennessee (TNNE); northwestern Tennessee (TNNW); southwestern Tennessee (TNSW); Texas (TX), and Wisconsin (WI). IDs with prefixes of M-R, AC-R, D-R, H-R, MC-R, and P-R are the numbers from the right ear tags of raccoons from The Edward J. Meeman Biological Station, and the grids at the Ames Plantation at Afternoon Course, Dusco Place, Hancock Place, Morning Course, and Pattersonville, respectively. The remaining columns are the numbers of bases in the pairs of alleles for microsatellite loci G10B, G10C, G10X, Pfl4, Pfl9, Pfl11, Pl-35, Pl-40, and Pl-61. A zero in one of these columns designates an allele for which a size could not be confidently assigned.

153

## LIST OF FIGURES

CHAPTER	PAGE
<b>I. An Assessment of Long-Term Residency and Temporal Composition in a Population of Raccoons (<i>Procyon lotor</i>).</b>	
<b>FIG. 1.</b> —Turn-over rates of raccoons ( <i>Procyon lotor</i> ) by sex and age class at the Meeman Biological Station in western Tennessee. Of (n) individuals in each sex and age class captured during any winter from 1991 to 2003, the proportion not recaptured the following winter is the turn-over rate. Each individual was considered as a separate independent trial. See text for explanation of age-class categories.	18
<b>II. Genetic Structure in the Raccoon (<i>Procyon lotor</i>) at Local to Transcontinental Scales.</b>	
<b>FIG. 1.</b> —Locations (●) for samples of raccoons ( <i>Procyon lotor</i> ) used in a study of genetic structure within the United States and Canada. See text for explanations of abbreviations for states.	48
<b>FIG. 2.</b> —Most probable genetic clusters, identified by program <i>Structure</i> , for individual raccoons ( <i>Procyon lotor</i> ) from sites at different geographic scales in the United States and Canada. Within each graph, individuals are grouped by their locations. Each shade represents the genetic pattern typical of a particular cluster, and each narrow vertical bar represents a single individual and the proportions of its genotype representative of each of the genetic clusters. Modal number of clusters (K) identified is 2 at each scale except K=4 for the southeastern area. See text for abbreviations for the sites, and explanations. a) Grids in southwestern Tennessee; populations 1-6 were AC, D, H, M, MC, and P, respectively. b) Grids in southwestern Tennessee (Ames) without Meeman; populations 1-5 are AC, D, H, MC, and P, respectively. c) Sites in the southeastern area; populations 1-9 are AR, GA, IN, KYE, KYW, SC, TNNE, TNW, and TNSW, respectively. In this graph, white represents a cluster that did not dominate any of the sampled populations of the southeastern area. d) Transcontinental states after the removal of the samples from Oregon; populations 1-13 are AL, AR, GA, IN, KS, KY, LA, MB, NYVT, SC, TN, TX, and WI, respectively.	63
<b>III. Spatio-temporal Dispersion of Kin Groups of the Raccoon (<i>Procyon lotor</i>).</b>	
<b>FIG. 1--</b> Locations of the Edward J. Meeman Biological Station (E. J. M. B. S) and the Ames Plantation (A. P.) in southwestern Tennessee, USA. AR, MS, and TN are Arkansas, Mississippi, and Tennessee, respectively. Symbols represent sites of trapping grids used in a study of temporal and spatial	



dispersion of closely related raccoons (*Procyon lotor*) across varied habitats and environmental conditions from 1991 to 2009. Grids at the Ames Plantation are, clockwise from left to right: Dusco Place, Pattersonville, Hancock Place, Afternoon Course, and Morning Course (from Carver 2009).

93

**FIG. 2--**Distance between mean locations of captures of individuals within dyads of full sisters or full brothers in the raccoon, *Procyon lotor*, determined as part of a study of the temporal and spatial dispersion of closely related raccoons across varied habitats and environmental conditions in southwestern Tennessee from 1991 to 2009.

98

**FIG. 3--**Spatial genetic autocorrelation generated by the program, *GenAlEx* for microsatellite loci in the raccoon, *Procyon lotor*. Results were produced as part of a study of the temporal and spatial dispersion of closely related raccoons across varied habitats and environmental conditions in southwestern Tennessee from 1991 to 2009. Solid shapes designate the multilocus autocorrelation coefficient,  $r$ , indicating the genetic similarity between pairs of individuals with geographic separation falling within a specified distance classes of increasing sizes and at what distance positive autocorrelation declines. Vertical bars delimit the 95% bootstrapped confidence interval for  $r$ . Hollow shapes designate upper and lower limits (U and L, respectively) of the 95% permuted confidence interval around 0, assuming no spatial genetic correlation. If the calculated  $r$ -value falls outside the permutational confidence limits around 0 and the bootstrapping confidence interval around  $r$  does not include  $r = 0$ , then significant spatial genetic structure is inferred. Vertical overlap between the bootstrapped confidence intervals indicate that the values of  $r$  for the different groups of individuals within a given distance class are not significantly different. a) Females, and b) males. For a) and b),  $r_1$ ,  $r_{2-3}$ , and  $r_{4-5}$  are the autocorrelation coefficients among raccoons of age class 1, grouped age classes 2 and 3, and grouped age classes 4 and 5, respectively. c) Females, and d) males. For c) and d),  $r_d$  and  $r_w$  designate the autocorrelation coefficients among raccoons captured during the dry period and the wet period, respectively. See the text for further explanation of the analysis.

102

## Appendix I

**FIG. 1.—**Rates of 1<sup>st</sup> appearance of raccoons (*Procyon lotor*) by sex and age class at the Meeman Biological Station in western Tennessee. Of (n) individuals in each sex and age class captured during any winter 1991-2004, the proportion not captured the previous winter is the percent of first appearance. The same individual could be present during more than 1 year in the same or different age class and was counted and used in the calculations again each additional year it was present. See text for explanation of age-class categories.

131

### Appendix III

**FIG. 1.**—Plots of Mantel test correlations between geographic distance in km and log Nei genetic distance between pairs of populations based on 8 microsatellite loci for raccoons (*Procyon lotor*) sampled in a study of genetic structure at different geographic scales across the United States and Canada. a) Transcontinental regions comprising the Northwest (NW), including Oregon only; Northern Midwest, including Manitoba and Wisconsin; Northeast, including New York and Vermont; East Central, including Indiana, Kentucky, and Tennessee; Southern Midwest, including Texas, Louisiana, Arkansas, and Kansas; and Southeast, including Alabama, Georgia, and South Carolina. b) Transcontinental regions as above but excluding the Northwest region. c) Transcontinental states; these comprise the same states as used in the transcontinental regions but with distances calculated among individual states rather than among regions. d) Transcontinental states as above but excluding Oregon (NW). e) Sites in the southeastern area, comprising Arkansas, Georgia, Indiana, eastern Kentucky, western Kentucky, South Carolina, northeastern Tennessee, northwestern Tennessee, and southwestern Tennessee. f) Trapping grids in southwestern Tennessee, comprising that at the Edward J. Meeman Biological Station, and the grids at Ames Plantation at Afternoon Course, Dusco Place, Hancock Place, Morning Course, and Pattersonville. g) Trapping grids in southwestern Tennessee (SW TN) as above but excluding that at the Edward J. Meeman Biological Station (Meeman).

148

## **Chapter I: Introduction**

Broadly applied population-genetics theory based on the island model assumes equal dispersal among subpopulations for both sexes and random mating within subpopulations (Wright 1943). However, at the local level, behaviors such as unequal dispersal between the sexes (Greenwood 1980; Handley and Perrin 2007), clustering of kin (usually of 1 sex), and nonrandom mating systems can promote the development of gregariousness and dominate genetic patterns (Hamilton 1964; Greenwood 1980; Chesser 1991a; Sugg et al. 1996). These patterns have been demonstrated by formal models (Chesser 1991a, b; Chesser et al. 1993) that have been applied to semi-gregarious (van Staaden et al. 1994) and gregarious mammalian species (Dobson et al. 1998, 2004; Pope 1998) including humans (Long et al. 1998). At regional and continental scales, the island model might be more appropriate and gene flow in opposition to genetic drift can produce a pattern of genetic differences positively correlated to geographic distance (isolation by distance, or IBD; Wright 1943).

Natal dispersal among males and philopatry (site fidelity to the natal home range) among females is the predominant pattern in both gregarious and solitary mammals (Greenwood 1980; Waser and Jones 1983; Handley and Perrin 2007). However, the magnitude of temporal and spatial dispersion of related individuals over varied habitats and environmental conditions have not been previously examined in solitary mammals or most other mammalian species. For these species, little information is available on the relative influence of these factors on spatial genetic variability at different geographic scales.

The raccoon (*Procyon lotor*) is an interesting model species for testing hypotheses regarding the temporal and spatial extent of residency, dispersal and the associated genetic variability in solitary-mammalian carnivores, which are much more numerous than their gregarious counterparts (Bekoff et al. 1984; Gittleman 1989). The raccoon is a long-lived and highly mobile species (Haugen 1954; Gittleman 1986; Nowak 1991) and is among the largest of the carnivores that can be recaptured routinely enough for robust monitoring (Gehrt and Fritzell 1996). At least for restricted periods of favorable environmental conditions and in preferred habitats, female raccoons have been found to remain as residents on sites for multiple years and to display clustering of close relatives (Ratnayeke 1997; Gehrt and Fritzell 1998a, b; Ratnayeke et al. 2002). This pattern is suggestive of lineage formation that would facilitate the development of gregariousness in a solitary carnivore (Ratnayeke 1997; Gehrt and Fritzell 1998a, b; Ratnayeke et al. 2002). However, raccoons live in wide variety of habitats (Lotze and Anderson 1979) and disappearance of individuals from sites is rapid in most studies (Johnson 1970; Moore and Kennedy 1985; Stevens et al. 1995; Maris 1998). Currently, the spatial and temporal extents of dispersal and residency in varied habitats and environmental conditions are unclear for solitary mammals including the raccoon.

Raccoons have greatly increased their distribution and abundance since the 1940's (Sanderson 1987). In this species, rate of dispersal is of special interest because it affects the speed of the spreading of epidemics such as raccoon rabies, which is the largest epizootic on record (Cullingham et al. 2009). Rate of dispersal also affects the speed of range extension or recolonization of sites vacated by removal of raccoons in efforts to reduce: 1) the spread of such disease, 2) predation on species of conservation concern

(Garrott et al. 1993; Jennings et al. 2006), 3) conflicts with humans in urban settings, and 4) damage to crops (Gehrt 2003).

The objective of this study was to assess the dispersion of related raccoons and the associated patterns of genetic variation across diverse habitats and environmental conditions over extended spatial and temporal spans. Specifically, the following predictions were tested for raccoons: 1) long-term residency is common for individuals; 2) the prevalent form of spatial dispersion of first order relatives across varied habitats and environmental conditions is in simultaneous multi-year clusters (Ratnayeke 1997; Gehrt and Fritzell 1998a, b; Ratnayeke et al. 2002); 3) such spatial dispersion of kin is associated over multiple years with varying environmental conditions (Gehrt 2003); 4) genetic differences increase directly with increasing geographic distances among local, regional, and transcontinental sites in accordance with IBD; and 5) migrants among sites at each scale are predominantly males. Also, long-term (annual) turn-over rates for the species, the distance of dispersion of male compared to female relatives, and the prevalence of lineages that immigrated as a unit were assessed. These predictions were tested using: 1) demographic data from 839 raccoons captured 1870 times between 1991 and 2009 on 6 study sites separated by a maximum of 80 km and comprising a total of 13.8 km<sup>2</sup> in southwestern Tennessee, and 2) microsatellite genotypes of 440 of these individuals captured between 2000 and 2009 and 215 individuals from other sampling sites spanning the United States and Canada. This study provides novel and needed insight on the structuring and dynamics of populations and genetics of raccoons and similar mammals.

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## **CHAPTER II: An Assessment of Long-Term Residency and Temporal Composition in a Population of Raccoons (*Procyon lotor*)**

Patterns of residency (habitation) and temporal mobility (annual turn-over) of individuals can have profound effects on the structure and dynamics of populations (see Anderson 1970; Handley and Perrin 2007; Ratnayeke et al. 2002; Waser and Jones 1983). Among mammals, there is a generalization of natal dispersal among males and philopatry (site fidelity to the natal home range) among females which results in temporal changes in compositions of populations (Greenwood 1980; Handley and Perrin 2007; Waser and Jones 1983). Mammalian dispersal has been widely studied, but philopatry and other extended patterns of residency and turn-over have not (Handley and Perrin 2007; Waser and Jones 1983). Questions remain relating to the frequency of long-term residents and dynamics of populations over multiple years. Overall, long-term investigations, needed to more clearly understand structure and dynamics of populations, are lacking for most groups of mammals.

The raccoon (*Procyon lotor*) makes an interesting model for studying long-term residency and rates of turn-over in natural populations. Female raccoons are typified as philopatric both by direct observation (Fritzell 1978a; Gehrt 2003; Ratnayeke 1997; Ratnayeke et al. 2002) and genetic analysis (Ary 2003; Cullingham et al. 2008; Ratnayeke et al. 2002), and, reproductively mature males may remain in the same area for at least a year (Fritzell 1978a, b; Gehrt 2003; Sumners and Kennedy 1995). However, the duration over which philopatry and other forms of residency commonly extend is unclear, and high annual turn-over rates (the percentage of all individuals found on a site during a year that are not found there the following year) have been generally observed in populations of this species (Johnson 1970; Maris 1998; Moore and Kennedy 1985;

Stevens et al. 1995). Gehrt (2003) surmised that higher rates of long-term site fidelity might occur when resources were predictable between years but annual dispersal of raccoons might occur when resource availability changes. At this time, residency for raccoons remains unclear.

*Procyon lotor*, a long-lived and highly mobile species (Gittleman 1986; Haugen 1954; Nowak 1991), lives in a variety of habitats (Lotze and Anderson 1979) and is among the largest of the carnivores that can be routinely captured, marked, released, and recaptured. Additionally, the species exhibits considerable ecological, sociological, and economic importance in natural and human-impacted ecosystems (see Crooks and Soule 1999; Gehrt 2003; Rogers and Caro 1998; Sanderson 1987) and is known to be dramatically increasing in population abundance throughout its distribution (Sanderson 1987). Estes (1996) indicated that medium-sized predators could impact many aspects of ecosystems, and Meffe et al. (1997) pointed out that predators play an important role in structuring biological communities. Additionally, information is lacking on individuals that belong to multiple cohorts of long-term residents (Johnson 1970). Therefore, raccoons make a valuable model for studying residency and turn-over in population structure.

The purpose of this study was to assess long-term residency of individuals and their temporal composition for a population of *P. lotor*. Specifically, the prediction was tested that long-term residency is common for individuals. Additionally, long-term (annual) turn-over rates for the species are presented for the first time. This study provides new and needed insight toward understanding structure and dynamics of mammalian populations.

## MATERIALS AND METHODS

*Study Area.*—This investigation was performed on a non-hunted site at The University of Memphis' 252 ha Meeman Biological Station (hereafter termed Meeman) described by Ladine (1995, 1997), 17 km north of Memphis, Shelby Co., Tennessee. Annual-precipitation data were obtained from archives at the National Climate Data Center (NCDC, Asheville, North Carolina), and those used for Meeman were originally recorded from the weather station at the Memphis International Airport. A 5 by 10 array of raccoon-sized Havahart (Woodstream Corporation, Lititz, Pennsylvania) or Tomahawk (Tomahawk Live Trap Co., Tomahawk, Wisconsin) live traps was spaced at about 150 m intervals across a landscape including upland and bottomland forests, oldfields, kudzu, ponds, and permanent and intermittent streams (Baldwin 2003; Carver 2009, Ladine 1997). This long-term grid was operated during a session each winter-breeding season from 1991 through 2004. A session consisted of about 2000 trap nights. A trap night is 1 trap operated for 1 night.

*Capture protocol.*—Methods followed the guidelines for the use of wild mammals in research suggested by the American Society of Mammalogists (Sikes et al. 2011) and were approved (IACUC Protocol #0016) by the Institutional Animal Care and Use Committee of The University of Memphis. When animals were first captured, they were immobilized as needed by intramuscular injection of 0.10 mg ketamine hydrochloride (Ketaset, Bristol Laboratories, Syracuse, New York; Vetalar, Ketalar, Parke-Davis, Detroit, Michigan) and 0.02 mg acepromazine maleate (The Butler Company, Columbus,

Ohio) per kg body weight. A Monel #3 tag (National Band and Tag Co., Newport, Kentucky) with an identification number was attached to each ear (2 tags per raccoon). Universal Transverse Mercator location codes, sex, reproductive condition, mass, lengths of the total body, tail, hind foot, and ear were recorded. Based on tooth wear, animals were assigned to the following age classes (Grau et al. 1970): age classes 1 (0-14 mo); 2 (15-38 mo); 3 (39-57 mo); 4 (58-86 mo); and 5 (>86 mo).

*Data analysis.*—Individual turn-over time was the span of years taken for an animal to disappear from the site. Annual turn-over rate (disappearance rate) was the percentage of animals present on a site during 1 year but not the following years. Long-term residents were those individuals detected on a site over a minimum of a 24-month span (portions of at least 3 breeding seasons). Individuals remaining over such an extended span were specifically investigated because any raccoon remaining on the same site for 2 or more years was likely to contribute more reproductively to the composition and genetics at the site, including the potential development of local lineages, as opposed to patterns resulting from higher turn-over and random breeding (Chesser 1991; Gehrt and Fritzell 1998a; Ratnayeke et al. 2002; Waser and Jones 1983). Contributing to this effect, young raccoons generally reared fewer offspring before their second or third breeding seasons (Dew 1978; Fritzell 1978a; Gehrt 2003; Gehrt and Fritzell 1999; Johnson 1970).

Correlation between amount of precipitation and numbers of individuals establishing long-term residencies was determined using Pearson's  $r$  (Conover 1999). Each individual was considered a separate independent trial (replicate) regarding whether or not it remained on the grid from 1 winter breeding season to the next (annual turn-over rate) or to the 3<sup>rd</sup> breeding season (long-term residency) for the purposes of Chi-squared tests.

Pearson's Chi-squared tests or 1-tailed Fisher's exact tests were used to determine whether differences existed in probabilities of turn-over or of becoming long-term residents among age classes, sexes, or years (Conover 1999; Zar 1974). Significance of differences among years or age classes for mean individual turn-over times was determined by Kruskal-Wallis tests (Conover 1999; Zar 1974). All statistical tests were performed using SAS 8.2 (SAS 2001). In analyzing turn-over times, animals first captured after 2000 were excluded, and turn-over times beyond 3 years were lumped into a single category for animals remaining 4 or more years. This was to avoid biases that might arise by recording individual persistence as being curtailed at the end of the regular study in 2004 though the animal might still remain on the site. For statistical tests of differences among years or groups of raccoons, long-term residency or turn-over time measures were included only from the first year the animal was captured to avoid a violation of the assumption of independence of samples.

To increase sample size and effectively test for equivalency of turn-over rates and times of different age and sex classes, age class 2 was combined with 3 and 4 with 5 to produce re-formed age classes 2+3 and 4+5, respectively, because a preliminary survey of the data suggested that the turn-over rates and times within these combined classes were very similar. Rate of appearance and disappearance for each age and sex classification was determined. If the same animal was present during more than 1 year in the same age class, it was counted 1 time for each year it was present, and it was considered to have disappeared if it was not caught the following year regardless of whether it was again captured in subsequent years. Rate of first appearance for 1991 and

rate of last appearance for 2004 were unknown because these animals could have been present before or after the study period, respectively.

## RESULTS

Data were analyzed from 277 raccoons captured 816 times over 14 years during the winter trapping sessions. The number of individual raccoons captured annually varied more than 3-fold with a low of 14 in 1994 and a high of 45 in 1996 (Table 1).

*Long-term residents.*—Of 215 raccoons first captured during a year from 1992 to 2002, 26 remained on the grid for at least 24 months (3 winter breeding seasons) to become long-term residents. The proportion of the individuals first captured during a year from 1992 to 2002 that became long-term residents varied from 0.0 to 18.9%, with a mean of 12.1% (Table 1). Groups of long-term residents tended to originate in distinct cohorts interspersed with gaps of several years. An extraordinarily high number of raccoons first captured during 2 years at Meeman remained to become long-term residents (Table 1): 7 (18.9%; 3 males and 4 females) in 1996 and 6 (18.8%; 3 males and 3 females) in 2001. This number did not exceed 2 in any other year, and was 0 in 1994 (Table 1). Of the individuals that remained 3 or 4 years on the grid, 8 of 11 (72.7%) and 3 of 4 (75%), respectively, established their residencies during 1996 or 2001 and the remainder originated their 3-and-4-year residencies the year before or after these 2 years.

Annual precipitation at Meeman averaged 143.0 cm but varied more than two-fold (94.7-193.5 cm) across the 13 years from 1991 to 2003, with highs near the years that the most raccoons began their long-term residencies. The 4 highest annual precipitation totals

**TABLE 1.**—Trends from 1992 to 2002 in long-term residency and turn-over rates of raccoons (*Procyon lotor*) from winter to winter and annual precipitation at the Meeman Biological Station (Meeman) in western Tennessee. Values in table are: 1. The number of individuals 1st captured each year on the Meeman grid; 2. The number of individuals 1st captured each year on the Meeman grid that became long-term residents by remaining on the grid over a total span of 3 breeding seasons (2 yr. minimum turn-over time); 3. The remainder of individuals 1st captured each year on the Meeman grid that disappeared from the grid before becoming long-term residents; 4. Percent of those individuals 1st captured each year on the Meeman grid that remained to become long-term residents; 5. Number of all individuals captured each winter from 1991 to 2003; 6. Number of all individuals captured each winter that were also captured the following year; 7. Number of all individuals captured each winter that were not captured the following year; 8. Percent of all individuals captured each winter that were also captured the following year; 9. Percent of all individuals captured each winter that were not captured the following year (annual turn-over rate); 10. Numbers of individuals of combined age classes 2 through 5 first appearing on the grid during a year; and 11. Annual cm of precipitation at Meeman. Each individual was considered as a separate independent trial.

	Year						
	1991	1992	1993	1994	1995	1996	1997
1. Number 1st captured	---	21	16	8	28	37	13
2. Number of long-term residents	---	2	1	0	2	7	2
3. Number resident < 2 years	---	19	15	8	26	30	11
4. % long-term residents	---	9.5	6.3	0	7.1	18.9	15.4
5. Number of all captured	28	24	20	14	29	45	28
6. Number returning next year	3	5	5	0	8	6	14
7. Number not returning	25	19	15	14	21	39	14
8. % returning next year	10.7	20.8	25.0	0.0	27.6	13.3	50.0
9. Turn-over rate, %	89.3	83.3	75.0	100.0	72.4	86.7	50.0
10. Age 2-5 first appearing	---	18	11	5	28	29	11
11. Annual precipitation, cm	150.1	119.8	111.8	125.7	144.5	193.5	182.6

**TABLE 1.**—Continued. Trends from 1992 to 2002 in long-term residency and turn-over rates of raccoons (*Procyon lotor*) from winter to winter and annual precipitation at the Meeman Biological Station (Meeman) in western Tennessee.

	Year							Total
	1998	1999	2000	2001	2002	2003	2004	
1. Number 1st captured	20	20	11	32	9	---	---	215
2. Number of long-term residents	1	2	2	6	1	---	---	26
3. Number resident < 2 years	19	18	9	26	8	---	---	189
4. % long-term residents	5	10	18.2	18.8	11.1	---	---	12.1
5. Number of all captured	36	31	19	36	19	29	---	358
6. Number returning next year	11	7	3	10	8	8	---	88
7. Number not returning	25	24	16	26	11	21	---	270
8. % returning next year	30.6	22.6	15.8	27.8	42.1	27.6	---	24.6
9. Turn-over rate, %	69.4	77.4	84.2	72.2	57.9	72.4	---	75.4
10. Age 2-5 first appearing	17	13	11	27	8	13	6	197
11. Annual precipitation, cm	131.6	115.6	94.7	167.7	190.1	132.0	---	



of any of the 14 years for Memphis were during 1996-7 (193.5 and 182.6 cm, respectively) and 2001-2 (167.7 and 190.1 cm, respectively--Table 1). Of the 215 individuals first captured each winter session from 1992 to 2002, the number that became long-term residents (0-7 per year; total of 26) by remaining on the grid at least 24 months or 3 breeding seasons was compared with the total centimeters of rainfall for that year and the following year (Table 1). The correlation,  $r$ , between the paired measures, was 0.6721 and the value differed significantly from 0 ( $P = 0.0235$ ) for a 2-tailed test. The relationship between turn-over rate and centimeters of rainfall for a given year was not as clear ( $r = -0.4418$ ;  $P = 0.1306$ ). The turn-over rate was not especially low for the first year of each wet period (39 out of 45 individuals or 86.7% in 1996; 26 out of 36 or 72.2% in 2001; 249 out of 329 or 75.7% over all years—Table 1). However, the 2<sup>nd</sup> wet year of each wet period had the 2 lowest turn-over rates for raccoons at Meeman from 1991 to 2003 (14 out of 28 or 50.0% in 1997; 11 out of 19 or 57.9% in 2002), allowing some individuals to extend their tenure to become long-term residents. Likewise, the highest numbers of individuals in combined age classes 2 through 5 (subadults and adults) first appeared on the grid (immigrated) on the year before or the first year of each wet period (28, 29, and 27 individuals in 1995, 1996, and 2001, respectively; total of 178 and mean of 16.2 across all years), but these numbers were not otherwise clearly related to precipitation levels (Table 1).

For data lumped across years and sexes, proportions of raccoons first captured during a year that became long-term residents varied from 2.8% (1 out of 36 individuals) for age class 1 to 20.0% for age class 5 (2 out of 10 of individuals--Table 2). Long-term residents

first captured in age-classes 1 and 5 were all females. Each individual was considered as a separate independent trial, and no significant differences in probability of becoming long-term residents were detected among individual age classes ( $\chi^2_4 = 6.0746$ ;  $P = 0.1936$ ). However, a Fisher's exact test indicated ( $P = 0.0432$ ) that significantly lower proportions of age class 1 raccoons became long-term residents than did individuals of lumped age classes 2 through 5 (25 out of 179 individuals or 14.0%). For all lumped ages and years, a lower proportion of males (10 out of 130 individuals or 7.7%) than females (16 out of 85 individuals or 18.8%) became long-term residents (Table 3), and the difference between sexes was significant ( $\chi^2_1 = 5.9903$ ;  $P = 0.0144$ ).

*Turn-over rates, comparison among years and cyclicity.*—The annual turn-over rates for raccoons at Meeman were high, averaging 75.4% and varying between 50.0% and 100.0% (14 out of 28 and 14 out of 14 individuals, respectively) from 1991 to 2003

**TABLE 2.**—Trends in long-term residency of raccoons (*Procyon lotor*) by age class at the Meeman Biological Station in western Tennessee. Values in table are: numbers of all individuals captured from 1992 to 2002 that were of each age class at first capture (sample size); those first capture raccoons that became long-term residents (those captured on the grid over at least 24 months or 3 breeding seasons); those that were resident for less than 24 months (3 breeding seasons) and so did not become long-term residents; and percent of first captures becoming long-term residents. See text for explanation of age-class categories.

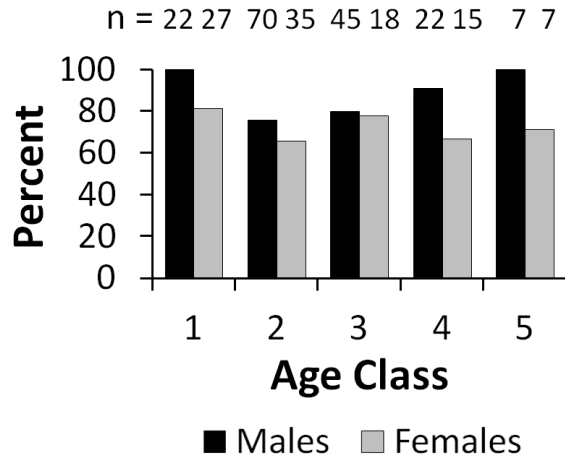
Trend	Age Class					Total
	1	2	3	4	5	
Number 1st captured	36	82	57	30	10	215
Number of long-term residents	1	14	5	4	2	26
Number resident < 2 years	35	68	52	26	8	189
% long-term residents	2.8	17.1	8.8	13.3	20.0	12.1

**TABLE 3.**—Trends in long-term residency of raccoons (*Procyon lotor*) by sex at the Meeman Biological Station in western Tennessee. Values in table are: numbers of all individual raccoons of each sex first captured from 1992 to 2002 (sample size); those that became long-term residents (captured on the grid over at least 24 months or 3 breeding seasons); those that were resident for less than 24 months (3 breeding seasons) and so did not become long-term residents; and percent of first captures becoming long-term residents. See text for explanation of age-class categories.

Trend	Sex		
	Males	Females	Total
Number 1st captured	130	85	215
Number of long-term residents	10	16	26
Number resident < 2 years	120	69	189
% long-term residents	7.7	18.8	12.1

(Table 1). After lumping all sex and age classes, no significant differences were revealed among the turn-over rates of the different years of the study ( $\chi^2_{12} = 9.2324$ ;  $P = 0.6830$ ). This also precluded significant values for tests for regular cycling in turn-over rates. Runs of rising and falling values of capture numbers and turn-over rates from year to year occurred irregularly, with lowest turn-over rates 2-5 years apart and highest turn-over rates 2-4 years apart (Table 1).

*Turn-over rates, comparison among sex and age classes.*—Turn-over rates were 100.0% (22 of 22 individuals) for age class 1 males, 90.9% (20 out of 22) for age class 4 males, and 100% (7 out of 7) for age class 5 males (Fig. 1). On the other hand, turn-over rates were considerably lower and more variable for males in age classes 2 and 3 and females in all age classes. For females, comparison between the turn-over rates of age class 1 (22 out of 27 individuals or 81.5%) and lumped age classes 2 and 3 (37 out of 53



**FIG. 1.**—Turn-over rates of raccoons (*Procyon lotor*) by sex and age class at the Meeman Biological Station in western Tennessee. Of (n) individuals in each sex and age class captured during any winter from 1991 to 2003, the proportion not recaptured the following winter is the turn-over rate. Each individual was considered as a separate independent trial. See text for explanation of age-class categories.

or 69.8%) revealed no significant differences ( $\chi^2_1 = 1.2584$ ,  $P = 0.2620$ ). The same was true when females of lumped age classes 2 and 3 were compared with those from lumped age classes 4 and 5 (15 out of 22 or 68.2%;  $\chi^2_1 = 0.0194$ ,  $P = 0.8892$ ). For males, turn-over rates for age class 1 were significantly different ( $\chi^2_1 = 5.8667$ ;  $P = 0.0154$ ) than those for lumped age classes 2 and 3 (89 out of 115 individuals or 77.4%). Differences in turn-over rates only approached significance ( $\chi^2_1 = 3.3604$ ;  $P = 0.0669$ ) when males of lumped age classes 2 and 3 were compared with those from lumped age classes 4 and 5 (27 out of 29 or 93.1%). All females had lower turn-over rates compared with males of the same age class but turn-over rates of males of lumped age classes 2 and 3 did not differ significantly from those of all female age classes lumped together (74 out of 102 or 72.5%;  $\chi^2_1 = 1.1592$ ,  $P = 0.2816$ ).

*Rate of appearance and disappearance (turn-over).*—For juvenile males, the rate of last appearance was 100.0% and of first appearance was 89.9% for age class 2 males, compared with lower rates of 85.2% and 76.7%, respectively, for the same measures for females in these age classes (Table 4). In mid-aged animals, all rates were lower than for juveniles, with rate of first appearance for each age class generally being lower than but within 15% of rate of last appearance within each sex. Rates of appearance and disappearance of males for an age class are generally higher than those for females of the same age class. From age class 2 upward, rates of first appearance declined and the difference between this measure and rate of last appearance generally increased for both sexes and became particularly large in age class 5 females and age class 4 and 5 males. In the oldest females, rate of last appearance (turn-over) did not rise, but rate of first appearance declined markedly. In contrast, in males, the rate of first appearance did not change drastically in the oldest age classes, but rate of last appearance (turn-over) rose to 100%.

*Turn-over time, duration and comparison among years.*—The high annual turn-over rates at this site were reflected in short turn-over times, with captures of the great majority of raccoons not extending beyond their first year (Table 5). Among individuals first captured from 1991 to 2000, no age class 1 females were captured over a span of more than 24 months except 1 that remained for 10 years, and none of any other sex or age were captured over a span of more than 4 years. Greater proportions of females of both age class 1 (juvenile) and combined age classes 2 through 5 had longer turn-over times than males of these age categories. Only 1 out of the 19 females first captured as juveniles apparently on their natal home ranges from 1991 to 2000 skipped (was not

TABLE 4.—Comparison of rates of first appearance and last appearance (disappearance) among age and sex classifications for raccoons (*Procyon lotor*) at the Meeman Biological Station in western Tennessee. Of (n) individuals in each sex and age class captured during any winter 1991-2004, the proportion not captured the previous winter is the percent of first appearance and the proportion not captured the following winter is the percent of last appearance. The same individual could be present during more than 1 year in the same or different age class and was counted and used in the calculations again each additional year it was present. See text for explanation of age-class categories.

Age	<u>% first appearance (n)</u>		<u>% last appearance (n)</u>	
	Males	Females	Males	Females
1	100.0% (24)	100.0% (29)	100.0% (24)	85.2% (29)
2	89.9 (74)	76.7 (46)	75.7 (74)	75.6 (46)
3	71.4 (66)	56.7 (31)	77.4 (66)	67.9 (31)
4	60.7 (33)	54.2 (26)	80.6 (33)	64.0 (26)
5	57.1 (10)	24.0 (26)	100.0 (10)	56.0 (26)

**TABLE 5.**—Individual turn-over times (span of years taken for an animal to disappear from the site) of raccoons (*Procyon lotor*) captured at the Meeman Biological Station in western Tennessee from 1991 to 2000: total numbers of each sex first captured in each age class (1-5); numbers that were recaptured at maximum terms of residency (individual turn-over times) of 0-10 years; and mean individual turn-over time in years (and standard error). See text for explanation of age-class categories.

Sex and age class	Total number in age class	Number remaining to maximum term of residency (turn-over time in yrs) shown											Mean individual turn-over time (and S. E.) for age class	
		0 yr	1	2	3	4	5	6	7	8	9	10		
M1	16	16	0	0	0	0	0	0	0	0	0	0	0	0.00 (0.00)
M2	45	37	4	1	2	1	0	0	0	0	0	0	0	0.36 (0.14)
M3	35	29	5	0	0	1	0	0	0	0	0	0	0	0.26 (0.13)
M4	19	17	1	1	0	0	0	0	0	0	0	0	0	0.16 (0.12)
M5	7	7	0	0	0	0	0	0	0	0	0	0	0	0.00 (0.00)
F1	19	15	3	0	0	0	0	0	0	0	0	0	1	0.68 (0.52)
F2	24	17	3	0	3	1	0	0	0	0	0	0	0	0.64 (0.25)
F3	14	10	2	0	1	1	0	0	0	0	0	0	0	0.64 (0.34)
F4	15	10	2	2	1	0	0	0	0	0	0	0	0	0.60 (0.25)
F5	7	5	0	2	0	0	0	0	0	0	0	0	0	0.57 (0.37)
Total	201	163	20	6	7	4	0	0	0	0	0	0	1	

captured during) a year on the grid, possibly due to dispersal, and then was recaptured. However, this was the only juvenile female that was first and last captured over the span of 3 breeding seasons needed as a minimum to be able to skip the middle year, and she then remained on her natal home range on the grid until her total span was 11 breeding seasons, always being captured in an area  $450 \times 300$  m. ( $150 \times 300$  m except for 2 years). Of these juvenile females, 3 others first captured after 2000 on their apparent natal home ranges later were recaptured after at least 1 year of not being captured during a trapping session. Of these 3, 1 dispersed 1200 m across the grid by the time she was a yearling then skipped a minimum of 2 years and was recaptured at her natal home range on the grid during her 7<sup>th</sup> winter. The second of these juvenile females skipped 2 years, then was recaptured 600 m from the site of her initial capture. The third of these juvenile females remained on the grid as a yearling, then skipped a minimum of 1 year and was recaptured on her initial home range her 5<sup>th</sup> winter. These 3 were not recaptured during the subsequent year. Mean individual turn-over times did not differ significantly among years for males ( $T_9 = 7.9129$ ;  $P = 0.5430$ ) alone or for females alone ( $T_9 = 5.9127$ ;  $P = 0.7416$ ).

*Turn-over time, comparison among sex and age classes.*—Mean individual turn-over times were similar among all age classes of females and were higher than any male age class (Table 5). Males had highest turn-over times for age classes 2 and 3. No male that was age class 1 or 5 when it was captured during a trapping session was ever recaptured during a later session (turn-over time = 0). For males first captured at age class 4, only 1 each remained as long as 1 and 2 years. No significant differences in turn-over times



were found among re-formed age classes 1, 2+3, and 4+5 for males ( $T_2 = 4.3781$ ;  $P = 0.1120$ ) or for females ( $T_2 = 0.7716$ ;  $P = 0.6799$ ).

## DISCUSSION

The present investigation at Meeman was the longest uninterrupted capture-mark-recapture study on free-ranging raccoons at a single site. The robust sampling across multiple habitats of 277 raccoons captured 816 times over 14 years, during which capture numbers and environmental factors varied markedly, provided novel findings. The results did not support the prediction that long-term residents would be common, though trapping methods were used that generally have a high likelihood of recapturing raccoons that remain on a site (Gehrt and Fritzell 1996). However, long-term residents were revealed and their trends were quantified. Only 26 out of 215 raccoons (12.1%) first captured from 1992 to 2002 (0-7 per year) remained on the study site for 2-10 years and thus were considered long-term residents, unlike the findings of other studies (Gehrt and Fritzell 1998a, b; Ratnayeke 1997). Such long-term residents in the present study tended to establish their residencies at the beginning of 2-year periods of high precipitation (13 of 26—see also methods of Gehrt and Fritzell 1998a, b; Ratnayeke 1997); and to be female (16 of 26-- see also Fritzell 1978a; Gehrt 2003); and of combined age classes 2 through 5 (25 of 26-- so that only one was philopatric). Data from an extensive study that was conducted at a nearby site during the same time period (Carver 2009) revealed that for age class 1 raccoons, only 2 males and 1 female remained on their apparent natal home ranges for as long as 3 winters to become long-term residents.

The prediction that long-term residents would be common among raccoons at the study site was based on reports that female raccoons are philopatric (Fritzell 1978a; Gehrt 2003), most remained on a site for 2-3 years (Gehrt and Fritzell 1998a, b; Ratnayeke 1997) and reproductively mature male raccoons may also remain in the same area for years (Fritzell 1978a, b; Maris 1998). Examination of these data from female raccoons in eastern Tennessee (Ratnayeke, 1997) revealed that of 10 juveniles alive on their natal home ranges in eastern Tennessee their first winter, only 4 were there during their second winter (40.0%). Though others returned later, observations were not of sufficient duration to determine proportions remaining as long-term residents as defined by the present study. Most of these prior studies did not quantify strict residency of individuals on home ranges, but rather numbers remaining and distances moved on the entire study sites. Of female raccoons born on a site in south Texas, 11 of 12 (91.7%) were still detected within 0.11 to 1.38 km of their natal home ranges 2-3 years later (Gehrt and Fritzell 1998a). In some other species of birds or mammals, home ranges may overlap by 60-80% from year to year (Hellickson et al. 2008; Janmaat et al. 2009; Xu et al. 2009) or 40-65% of adults may be identified on the same breeding range as the previous year (Schjorring et al. 2000). In dolphins, 18% of individuals were noted as present every year at a site over a 10-year span (Parsons et al. 2006). In coyotes, which primarily associated as mated pairs or small groups of adults with pups, 28% of resident adults remained on the same home ranges for at least 21-33 mo. (comparable to our “long-term resident” criterion), and 12% of these remained 43-48 months, during a 50-month span of monitoring (Andelt 1985). Each year, 12-29% of males and 4-9% of females emigrated.

Patterns of long-term residency, including philopatry, have rarely been investigated in solitary carnivores. However, in black bears, females established long-term residencies either on or near their mothers' home ranges or after dispersal (Costello 2010; Rogers 1987), 8 of 10 radio-tracked males (80.0%) that were not lost resided on their mothers' home ranges through their second year of age but none through their third year (Costello, 2010); and some (Rogers 1987), or all (Costello 2010) males established long-term residencies after dispersal. Raccoons may have relatively short-term residencies and high turn-over rates in small areas but longer-term residencies in the larger region (Johnson 1970). Few accounts have been published on distances of shifts in home ranges of raccoons during consecutive years and such measures are likely biased because of the relative difficulty of locating the same individual both before and after it has made a large shift in home range (Gehrt 2003; Gehrt and Fritzell 1998a). Acknowledging this potential bias, for the small proportion of raccoons recaptured in consecutive years, most were found to have moved < 5 km in some studies (Rosatte et al. 2007, 2010); and in another study, 21% of 118 parous females to have moved < 1 km and 5.9% to have moved 1-3 km (Cullingham et al. 2008).

If raccoons shifted home ranges slightly away from edges of the grid that they previously had barely overlapped, but, without dispersal having occurred in any meaningful sense, it could explain some of the rarity of long-term residents and the high turn-over rates at Meeman. Such movements of raccoons have been seen elsewhere (Gehrt 2003) but were detected in only 15% of 33 radio-tracked adult raccoons on a site adjacent to the Meeman grid (Sumners 1992; Sumners and Kennedy 1995; Tabatabai 1988). In addition, very few females and no juvenile males in the present study moved

such a short distance and re-established a home range elsewhere on the grid. Apparently, dispersal distances for these classes of raccoons were typically greater than the 600 by 1350 m dimensions of the grid. In addition, only 4% ( $n = 8$ ) of the 202 raccoons first captured during a given year from 1991 to 2000 skipped (were not captured during) a following year and then were recaptured later. Such a skipped year does not appear likely to be due to shifting slightly off the grid because these raccoons were captured in traps at the edge of the grid only slightly more frequently (68.0% vs. 59.0%) the year before and after the year they skipped than were raccoons ( $n = 10$ ) that did not skip a year in captures over an equivalent time span. It is unlikely that such minor shifting of edges or complete home ranges (Sumners 1992; Sumners and Kennedy 1995; Tabatabai 1988) has appreciably reduced estimates of long-term residencies or inflated those of turn-over rates at Meeman.

High proportions of long-term residents have been previously reported for raccoons, but inspection of the data from these studies reveals that they were conducted over relatively short durations of 3 years or less, and near permanent water sources (Gehrt and Fritzell 1998a, b; Ratnayeke 1997) or during especially wet periods (NCDC, Asheville, North Carolina). These studies did not aim to examine the relationship between availability of surface water and long-term residency and were too brief to monitor patterns in multiple annual cohorts of long-term residents (Fritzell 1978a; Gehrt and Fritzell 1998a, b; Ratnayeke 1997). The current findings permitted generalization of such shorter term observations on raccoon residency by temporally spanning extended environmental patterns and multiple events of establishment of long-term residents, and by monitoring all areas of the grid with equal intensity, including uplands and areas

without regular water sources. At Meeman and at other sites in western Tennessee, raccoons foraged, denned, and were captured in traps more frequently in forested habitat and near water sources (Allsbrooks and Kennedy 1987; Baldwin 2003), consistent with findings of other studies (Fritzell 1978a; Kaufmann 1982); in the present study, consecutive years with wet weather closely matched prominent peaks in establishment of long-term residencies. The high numbers of long-term residencies established at Meeman early in each wet period (1996-7 and 2001-2) may have been buildups of the population from dry years just prior (NCDC, Asheville, North Carolina). During these dry years the lowest numbers in the 14-year span of captures and of raccoons remaining to the following years (in 1994 and 2000) were recorded, indicating depopulated home ranges.

Juveniles did contribute to the pulses of new raccoons occupying the Meeman site at the beginning of wet periods after these population lows—a total of 13 in 1996 and 2001 combined, out of a total of 35 juveniles captured over the whole 14 years. However, none of these 13 juveniles remained on the site as long as a year, unlike those in the population buildup in south Texas (Gehrt and Fritzell 1998a, b) so that the cohorts of long-term residents included no philopatric individuals. At other times, juveniles at Meeman more closely resembled those at south Texas and eastern Tennessee (Gehrt and Fritzell 1998a, b; Ratnayeke 1997; Ratnayeke et al. 2002) in that no males and some females (3 of 19) remained philopatric for 1 year; but differed in that only 1 female remained longer. Thus, at Meeman, the proportions of each sex of juveniles that became long-term residents were similarly lower than that of older raccoons of either sex though the turn-over rate of juvenile females was similar to that of older females and lower than that of juvenile males.

Raccoons (Fritzell 1978a) and other solitary carnivores (Rogers 1987) may establish home ranges, where they are vacated by previous residents of the same species, to gain access to resources including mates (Sandell 1989). These home ranges may be maintained if the habitat is favorable, especially where there are few other habitat options as is the case of scattered woodlots and water sources in primarily xeric or unforested habitat such as prairie (Beasley et al. 2007a, b; Chamberlain et al. 2007). All forms of long-term residency can benefit by familiarity with, and defense of predictable local resources (Gehrt 2003), including male access to breeding females (Costello 2010), and especially when competing with immigrants (Handley and Perrin 2007). Long-term philopatry can also benefit by kin cooperation (Handley and Perrin 2007) when survivorship is high and local matrilineal groups of related females develop (Gehrt 2003). Long-term home ranges may be abandoned and shorter-term residency become advantageous when resource predictability (Gehrt 2003) or availability declines, or to avoid inbreeding or kin competition (Handley and Perrin 2007). Raccoons may remain long-term when or where they are in prime habitat such as along longer-standing water bodies as it appears occurred in studies by Ratnayeke (1997), Ratnayeke et al. (2002), and Gehrt and Fritzell (1998a, b). In black bears, similar to the Meeman raccoons, the establishment of long-term home ranges was strongly pulsed, with about as many residencies (7) established during 1 year as in the 8 other years combined (average of 1 per year--Rogers 1987).

In addition to availability of water, other weather factors and disease may influence residency in raccoons. Severe winter weather can have major effects on raccoon demography (Johnson 1970; Ritke and Kennedy 1988; Sanderson 1987; Stuewer 1943). When an ice storm and other severe winter weather struck at Meeman in 1994, it was the

year of the lowest capture number (14) and highest turn-over rate of 100% (Ladine 1995; Maris 1998). Previous studies on or adjacent to the Meeman site found similar effects from low temperatures and snow covering food on the ground (Allsbrooks and Kennedy 1987; Moore and Kennedy 1985). However, turn-over and establishment of long term residencies during the current study appeared, in general, to have little relationship with heavy snowfall and low winter temperatures, which had milder means and extremes than in the prior 15-20 years in the Memphis area (NCDC, Asheville, North Carolina). Canine distemper in raccoon populations can cause high levels of mortality on approximately 4-year cycles (Hoff et al. 1974; Johnson 1970; Kaufmann 1982; Roscoe 1993), and was suspected at the Meeman site in 1997 (Maris 1998). However, turn-over rate and number of raccoons captured did not appear to be affected during that year nor by 4-year cycles.

The present long-term study supports the short-term results of Maris (1998) and Moore and Kennedy (1985) in indicating high annual turn-over rates (mean 76.4%) population-wide, and the range (50.0- 100.0%) from 1991 to 2003 encompassed much of the temporal or geographic plasticity in dispersal behaviors demonstrated by raccoons in or among shorter term studies. Duration and monitoring techniques differed greatly among studies, but annual turn-over rates were often on the order of 65-80% population wide (Fritzell 1978a; Johnson 1970; Maris 1998; Moore and Kennedy 1985). Ladine (1995) concluded turn-over was related to food resources. This may have been affected by precipitation, and the present study found residency and dispersal related to wet and dry periods. Landscape characteristics may affect dispersal behaviors geographically (Cullingham et al. 2009), and raccoon populations in northern states tend to have more rapid turn-over than those in the southern states (Johnson 1970). The tendency for each

sex to remain as residents or disperse varies geographically in some other species of mammals and birds (Foster and Endler 1999). Though turn-over rates were not found to differ significantly among years in raccoons on the Meeman site, the lack of statistical significance in this and some other tests in this study may be affected by the high variability in turn-over times and rates among individuals and sex and age classes, and the low proportions of animals in any of these classes at any year persisting to the following year. The sometimes large differences in values among these data classes present the appearance of biological significance but sample sizes were too small for statistical tests by year, sex and age.

The present study found immature raccoons to generally have higher turn-over rates than adults, similar to prior reports (Johnson 1970; Maris 1998; Moore and Kennedy 1985; Stevens et al. 1995). Unlike the present study, some others (Cullingham et al. 2008; Ratnayake et al. 2002) have reported male raccoons philopatric near their mothers. Some of these instances could alternatively have been of dispersal to a site near, but not overlapping, the natal home range; juveniles that were going to disperse before breeding; mothers and sons dispersing to the same site; or post-dispersal fathers sharing home ranges with daughters. Such alternatives could be similar to the situation in the current study, in which no juvenile males ( $n = 22$ ) remained to the point of their second winter or were likely to have reproductively contributed at the natal home range so that all age class 2 males ( $n = 70$ ) on the grid first appeared there at that age. Likewise, all juvenile male raccoons appeared to disperse in Texas (Gehrt and Fritzell 1998a, b). In such situations, the potential genetic consequences would have been quite different from those



of strict philopatry of breeding male and female relatives together on the natal home range.

The data for Meeman suggest that juvenile female turn-over rates are lower (dispersal is less frequent or over shorter distances) than for juvenile males. This was also true of most prior raccoon studies (Gehrt 2003), in which turn-over for juvenile females varied from 0.0 to 60.0% (Cullingham et al. 2008; Gehrt and Fritzell 1998a, b; Ratnayeke 1997; Stuewer 1943). This rate at Meeman was 78.9% (n = 19), and 76.7 % (n = 35) of age class 2 females captured were not captured as age class 1 females. The high rate in the present study in comparison to these prior studies may be due to temporal or geographic differences in demography or differences in methods such as the inclusion at Meeman of habitats and years with less available water. Most of these prior studies were along permanent water or during particularly wet periods. During some multi-year spans at Meeman, the turn-over rate for juvenile females was more comparable to that from other studies with about the same duration, but, over the full 14 years, the higher values from Meeman provided a more comprehensive range and mean for turn-over rates in that region and did not show the common philopatry of juvenile females reported in other studies (Fritzell 1978a; Gehrt and Fritzell 1998a, b; Ratnayeke 1997). Short-term monitoring may not detect some of the temporal variability within populations and lead to the appearance of great demographic differences reported among sites.

At Meeman, compared to the high turn-over rates (rate of last appearance) of the oldest and youngest age classes of males, adult rates for both sexes were generally more moderate (between about 65 and 80%) with the measure being higher for males than for females of the same age (Fig. 1). These trends were similar to those in other studies--

although females may remain philopatric (Fritzell 1978a; Gehrt 2003; Ratnayeke 1997; Ratnayeke et al. 2002) and reproductively mature males remain in the same area for at least a year (Fritzell 1978a, b; Maris 1998), both adult females (Cullingham 2008) and males (Kaufmann 1982) may also shift areas often, and the genetic patterns in populations are consistent with this balance (Ratnayeke et al. 2002). Sandell (1989) also claimed for solitary mammalian carnivores in general that reproductive-aged males should display a balance of roaming and residency as conditions change. In the present study, turn-over rates for males in age classes 1, 4, and 5, compared to those in age classes 2 and 3 and all females, were extremely high and invariant, suggesting that they are less responsive to changing factors on the site than the latter groups (Maris 1998).

Turn-over rates (percent of last appearance) may be due to both dispersal off the site (emigration) and mortality; whereas, rate of dispersal detected onto the site (immigration, or percent of first appearance) does not have this mortality component. Both the 100% turn-over in 1994 for the entire population (Ladine 1995; Maris 1998), and every year for juvenile males, seemed to be chiefly due to dispersal rather than regional mortality (Ladine 1995) because numerous new raccoons of both sexes and most ages appeared in 1995 (Ladine 1995; Maris 1998) and more new age class 2 males appeared annually than any other age and sex. In contrast, some other sites repopulated rapidly after artificial depopulation but not by elevated immigration (Rosatte et al. 2007). In juveniles, the lower rates in females than males indicated more philopatry (Table 4), consistent with other raccoon populations and mammalian species (Gehrt 2003; Greenwood 1980). Declining rates of first appearance with advancing age indicated that dispersal rates dropped and home ranges stabilized more in older females than males. Mortality was not

directly measured but may account for the much lower rate of first appearance vs. rate of last appearance for the oldest age class, particularly for males. Adult mortality is generally low, except by disease, and juvenile mortality higher, in raccoon populations exposed to little harvesting and few roads (Gehrt 2003).

The southeastern region of the U. S. A. is threatened by rabies, which constitutes the greatest epizootic in North America (Gehrt 2003; Cullingham et al. 2008). The spread of such diseases could be hastened by frequent dispersal (Coyne et al. 1989; Macdonald and Laurenson 2006) such as was observed at Meeman during all years for juvenile male raccoons, and for raccoons in general as depopulated home ranges (lowest number of captures) at the end of dry periods began to fill at the start of the wet periods (highest number of captures—Table 1). Disease control measures should be intensified in years or areas in which such rapid movement is expected (Cullingham et al. 2008, 2009). Rapid recolonization of vacated sites also complicates the control of nuisance raccoons (Gehrt 2003).

The generally low turn-over times at Meeman reflected the high turn-over rates. However, a few individuals had very long turn-over times and were notable because they could have facilitated the development of lineages, and thereby disproportionately influenced the structure of the population and its genetics. One female was captured annually on her home range longer than any other free-ranging raccoon--from her juvenile to her 11<sup>th</sup> winter season (10 year turn-over time) except for as a yearling, when she may have dispersed temporarily. Among the females, mean and standard error for turn-over times for age class 1 females would have been less than half of those of other age classes but for this 1 animal. In addition, interrupted annual trapping on this site after

2004 captured 4 juvenile females that were recaptured over spans of 4-7 breeding seasons but not during some middle sessions. A large proportion of the females that were detected on the Meeman site over a minimum of a 24-month (3 winter) span skipped a middle winter, and juvenile dispersal followed by a return to the natal home range was seen in a few female raccoons in eastern Tennessee (Ratnayeke 1997). In addition, females first captured at unknown ages in Alabama were recaptured a maximum of 7 years and 9 months later (Johnson 1970) and a female captured as a juvenile in Michigan was killed 800 m away 12 years later (Haugen 1954), but these may have vacated their natal sites in the interim.

The lower turn-over times for males than females at Meeman also reflected the patterns in the turn-over rates and the effect of the females with very long residencies. However, a male first captured at age class 3 was detected by the interrupted annual trapping on this site after 2004 to have been present on a similar section of the grid during 4 years across a span of 8 breeding seasons, which may be longer than any other free-ranging male raccoon reported. Mean individual turn-over times have rarely been reported for raccoons and most other studies were not of sufficient duration or regularity to determine the longer turn-over times (Johnson, 1970).

The present study was the longest uninterrupted investigation of free-ranging raccoons, with regular sampling spatially spanning multiple habitats and temporally spanning extended environmental patterns and multiple pulses of establishment of long-term residents. Studies of raccoons conducted primarily near water sources or during wet periods over shorter terms observed that high proportions of females remained philopatric and established matrilineal lines while juvenile males dispersed (Gehrt and Fritzell 1998a) and

also that nearby adult females were more genetically related than adult males (Ratnayeke 1997; Ratnayeke et al. 2002). However, the present study, with a duration and regularity of sampling that were sufficient to determine proportions and maximum spans of interrupted or uninterrupted residency across various habitats, provided several unique findings such as low levels of philopatry even in females, and long-term residency that was rare and episodic. These patterns would not facilitate: 1) lineage-structuring in the population or its genetics; 2) excess heterozygosity within lineages (Chesser 1991); or 3) the eventual development of cooperation or socialization within each lineage (Sugg et al. 1996) unless lineages disperse together, a circumstance that has not been documented for raccoons. Instead, these findings suggest a widespread mixing of the gene pool. Studies like the present one, conducted in other locations, might determine if intermittent cohorts and generally low numbers of long-term residents are typical of much of the raccoon's geographic range characterized by habitats with multi-year cycles in available water or other climatic fluctuations—e.g., wet periods spanning 1-2 years and associated with the El Nino Southern Oscillation climatic pattern occur every 3-7 years across most of the southern U. S. A. (Raven et al. 2010). Such studies might establish whether some of the demographic differences that shorter-term raccoon studies noted may stem from observation of only a subset of the temporal or spatial variability found in each population. These demographic patterns, including dispersal, may affect evolutionary processes (Chesser 1991; Greenwood 1980; Hamilton 1964; Ratnayeke et al. 2002) as well as disease control and conservation planning for solitary carnivores and the species they heavily impact (Garrott et al. 1993; Jennings 2007; Sugg et al. 1996). In addition, detailed genetics studies are needed to characterize the raccoon breeding system (Gehrt

2003), relative contributions of long-term residents to local genetics and temporal variation in lineage effects and to determine if portions of lineages disperse together, exhibiting group fidelity (Rood 1989; Waser et al. 1994).

## CONCLUSIONS

1. The present study was the longest uninterrupted investigation of free-ranging raccoons, with regular sampling spatially spanning multiple habitats and temporally spanning extended environmental patterns and multiple pulses of establishment of long-term residents.
2. Establishment of long-term residencies was infrequent, even among females, but was much more common during multi-year periods of high precipitation; a few individuals established very long-term residencies up to the record for free-roaming raccoons of 11 winters.
3. Only one philopatric juvenile established a long-term residency and that was a female.
4. Long-term residencies were established mostly by age class 2 males and females of combined age classes 2 through 5, and included fewer males than females overall.
5. Turn-over rates were high, varied greatly from year to year, and were 100% for the youngest and oldest males but lower for mid-aged males and for females of all age classes.
6. The very high turn-over rates that occurred in juveniles and after severe winter weather appeared to be due to dispersal rather than mortality.

7. In the oldest females, dispersal rates decreased and home ranges stabilized, as indicated by declining rates of first appearance.
8. Increased turn-over rates in the oldest class of males appeared to be due to mortality.
9. Frequent dispersal such as was observed at the end of dry periods, after severe winter weather, and during all years for juvenile males, could hasten the spread of diseases like raccoon rabies.
10. The observed low levels of philopatry and long-term residency would not facilitate lineage-structuring in the population or its genetics or the development of gregariousness within lineages.
11. Novel findings of the current study include substantial evidence of high turnover rates in a raccoon population, suggesting a widespread mixing of the gene pool and that site fidelity is not the norm.
12. Other extended studies are necessary to determine if low but extremely variable numbers of long-term residents are typical of many raccoon populations affected by strongly fluctuating conditions.

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### **CHAPTER III: Genetic Structure in the Raccoon (*Procyon lotor*) at Local to Transcontinental Scales**

Broadly applied population-genetics theory based on the island model assumes equal dispersal among subpopulations for both sexes and random mating within subpopulations (Wright 1943). However, through application of such theory, even species in which closely related individuals avoid mating with one another have sometimes produced inbreeding coefficients that are higher than expected for randomly breeding populations (Chesser 1991*a*; Sugg et al. 1996). At the local level, behaviors such as unequal dispersal between the sexes (Greenwood 1980; Handley and Perrin 2007), clustering of kin (usually of 1 sex), and nonrandom mating systems may dominate genetic structure as demonstrated by formal models (Chesser 1991*a, b*; Chesser et al. 1993) that have been applied to semi-social (van Staaden et al. 1994) and social mammalian species (Dobson et al. 1998, 2004; Pope 1998) including humans (Long et al. 1998). Such analyses have not been applied to species such as solitary mammals or carnivores that have less visible boundaries for populations and subpopulations.

These local genetic patterns influenced by sex-biased dispersal and non-random mating may be superimposed on a regional and continental background. At the latter scales, the island model may be more appropriate and has demonstrated that gene flow in opposition to genetic drift should have a major influence on genetic structure (Slatkin 1994). If physical or behavioral factors such as landscape barriers or corridors, clustering of kin, and long-distance dispersal do not induce irregularities in migration, isolation by distance (IBD) should be revealed by genetic differences positively correlated to geographic distance (Wright 1943). This association has been investigated in a large number of species (e. g., Hamilton and Kennedy 1987; Paetkau et al. 1997; Pope et al.

2006). For most species, little information is available on the relative influence of these factors on genetic structuring (spatial genetic variability) at different geographic scales.

The raccoon (*Procyon lotor*) is an interesting model organism for testing hypotheses relating to genetic structuring in solitary-mammalian carnivores, which are much more numerous than their gregarious counterparts (Bekoff et al. 1984; Gittleman 1989). With its intermediate body size, the scale of the raccoon's genetic patterns may be representative of those of other solitary carnivores which similarly have been described as displaying largely male-biased dispersal (Greenwood 1980). However, unlike some of those species, it is capturable enough for robust sampling (Gehrt and Fritzell 1996). In raccoons, rate of dispersal is of special interest because it affects the speed of the spreading of epidemics such as raccoon rabies, which is the largest epizootic on record (Cullingham et al. 2009). Rate of dispersal also affects the speed of range extension or recolonization of sites vacated by removal of raccoons in efforts to reduce: 1) the spread of such disease, 2) predation on species of conservation concern (Garrott et al. 1993; Jennings et al. 2006), 3) conflicts with humans in urban settings, and 4) damage to crops such as corn (Gehrt 2003).

Starting in the 1940's, raccoons greatly increased their distribution and abundance (Sanderson 1987) and today occur in a relatively continuous range including areas of the Rocky Mountains and western deserts where they were once uncommon or absent (Gehrt 2003). Of vital interest is the prevalence of movement and gene flow due to raccoons dispersing or being transported long-range by humans across such regions characterized by habitats that appear relatively inhospitable for these animals. Raccoons have been found to prefer forested riparian lowlands and rarely move across more xeric uplands

(Baldwin 2003; Baldwin et al. 2006; Kaufmann 1982). Also, genetic data and the spread of raccoon rabies suggest that large rivers may hinder dispersal (Cullingham et al. 2009; Smith et al. 2002). However, raccoons can move long distances (Lynch 1967; Priedert 1961; Rosatte et al. 2010; Tabatabai 1988) and live in a variety of habitats (Lotze and Anderson 1979) including those highly impacted by humans (Tabatabai 1988). The raccoon's distribution across a broad Nearctic range is among the most continuous for carnivores (Kaufmann 1982) suggesting that it may navigate most obstacles.

Genetic patterns across the raccoon's distribution could reveal major barriers to gene flow. In eastern North America, variation in the mitochondrial DNA of raccoons has been described but is maternally inherited (Cullingham et al. 2008a) whereas dispersal is primarily attributed to males (Gehrt and Fritzell 1998; Greenwood 1980; Ratnayeke et al. 2002). Variation was described in relatively low numbers of allozyme alleles in raccoons in the southeastern, midwestern, and northwestern United States (Beck and Kennedy 1980; Dew and Kennedy 1980; Hamilton and Kennedy 1987); and in microsatellite DNA in local populations in Illinois, New York, Ontario, Indiana, and Pennsylvania (Ary 2003; Cullingham et al. 2008b, 2009; Dharmarajan et al. 2009; Root et al. 2009).

The objective of this study was to determine the frequency of dispersal of each sex and genetic differences among sites at local, regional, and continental scales in a solitary carnivore. This goal was accomplished with the raccoon by the incorporation of sites in addition to those in previous studies, data from mark-recapture and live-trapping, and the use of microsatellite DNA, which is biparentally inherited and hypervariable. The current study should better detect the movements of males and the genetic variation across the range of the raccoon, which may reveal barriers to dispersal and consequent gene flow to

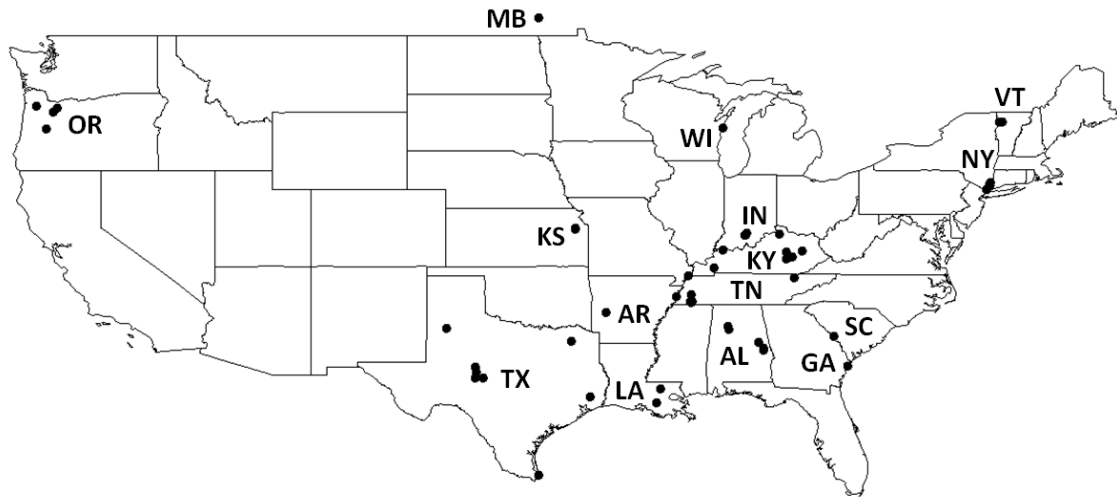


test the following predictions: 1) genetic differences increase directly with increasing geographic distances among local, regional, and transcontinental sites in accordance with IBD; 2) migrants among sites at each scale are predominantly males. Multi-scale information is lacking on genetic patterns and movements of each sex in raccoons for critical parts of their range (Hamilton and Kennedy 1987; Root et al. 2009). This study provides novel findings on structuring and dynamics of populations and genetics of raccoons and similar mammals.

## MATERIALS AND METHODS

*Sample collection.*—Samples of tissue were collected from the ears of raccoons from 6 live trapping grids in southwestern Tennessee during 2001-2006 and 2009 and preserved in 95% ethanol. Of these grids, 5 at the Ames Plantation (hereafter termed, “Ames”) were separated by a minimum of 1.5 km (mean 5.2 km) and the other one was 75 km northwest at the Meeman Biological Station (hereafter termed, “Meeman”).

Additional details about these study sites and trapping procedures can be found in Ladine (1995, 1997) and Vecchio (2011) for Meeman, and Baldwin (2003), Baldwin et al. (2006), Carver (2009), Carver et al. (2011), and Hisey (2012) for both Meeman and Ames. Methods followed the guidelines for the use of wild mammals in research suggested by the American Society of Mammalogists (Sikes et al. 2011) and were approved by the Institutional Animal Care and Use Committee of The University of Memphis (IACUC Protocol #0016, investigator M. L. Kennedy). Tissues from raccoons were also obtained via sportsmen from 3 other sites spanning Tennessee, and 12 other states and 1 province spanning the United States and Canada (Fig. 1). DNA was



**FIG. 1.**—Locations (●) for samples of raccoons (*Procyon lotor*) used in a study of genetic structure within the United States and Canada. See text for explanations of abbreviations for states.

extracted using the Puregene DNA Isolation Kit (Gentra Systems, Inc.) and quantified using a VersaFluor fluorometer (Bio-Rad Laboratories). PCR primers for microsatellite loci G10B, G10C, G10X (Paetkau et al. 1995), Pfl4, Pfl9, Pfl11 (Kays et al. 2000), Pl-35, Pl-40, and Pl-61 (Ary 2003) were used to amplify target sequences, which were genotyped on an ABI 3730xl DNA Analyzer (Applied Biosystems, Foster City, CA, 94404). Samples for which at least half of the alleles were readable were included in the analyses.

With the exceptions noted as follows, most analyses were performed at 3 geographic scales: 1) Transcontinental sites, each with minimal sample sizes of 5 individuals, comprised the following set of 1 Canadian province and 14 of the United States (each

with its state or province abbreviation for an identifier, and the sample size from that site): Alabama (AL, 6); Arkansas (AR, 11); Georgia (GA, 5); Indiana (IN, 6); Kansas (KS, 12); Kentucky (KY, 34); Louisiana (LA, 5); Manitoba (MB, 15); New York-Vermont (NYVT, 13); Oregon (OR, 15); South Carolina (SC, 6); Tennessee (TN, 500); Texas (TX, 13); and Wisconsin (WI, 15). To form NYVT, samples from eastern New York and western Vermont were lumped because only 2 samples were available from the latter. For certain tests particularly affected by small sample sizes, states were grouped into transcontinental regions. These comprised the following set with sample sizes of at least 13 (each with the sample size from that site): NW (Northwest, 15) included Oregon only; NMW (Northern Midwest, 30) included Manitoba and Wisconsin; NE (Northeast, 13) included New York and Vermont; EC (East Central, 540) included Indiana, Kentucky, and Tennessee; SMW (Southern Midwest, 41) included Texas, Louisiana, Arkansas, and Kansas; and SE (Southeast, 17) included Alabama, Georgia, and South Carolina.

2) At the scale of the southeastern area, the set of sites each had total sample sizes of at least 5 individuals taken from up to 4 lumped contiguous counties within Tennessee, Kentucky, and their directly adjacent states. Identifiers of sites (each with its sample size) were state abbreviations AR (11), GA (5), IN (6), and SC (6), and substate clusters of samples from eastern Kentucky (KYE, 13); western Kentucky (KYW, 16); northeastern Tennessee (TNNE, 20); northwestern Tennessee (TNNW, 21); and southwestern Tennessee (TNSW, 459). Some individuals that were from this area and included in the transcontinental set of samples were excluded from the southeastern area

analyses because they were not part of a cluster of nearby individuals from contiguous counties.

3) Sites at the local scale comprised the trapping grids at Meeman and Ames located within 3 contiguous counties in southwestern Tennessee. Identifiers of sites (each with its sample size) were M (152), for Meeman; and AC (43), D (79), H (110), MC (28), and P (29) for grids at Ames at Afternoon Course, Dusco Place, Hancock Place, Morning Course, and Pattersonville, respectively. To test hypotheses at local, area, and transcontinental scales, each site at a given scale was designated as a subpopulation and the group of sites as a population.

At each geographic scale, the microsatellite data were analyzed with the following programs. GENEPOP 4.0 (Rousset 2008) was used to perform tests for linkage disequilibrium and Hardy-Weinberg equilibrium (HWE) and to calculate  $F_{IS}$  at each locus at each site. GenAlEx 6.2 (Peakall and Smouse 2006) was used to calculate allele frequencies, expected and observed heterozygosity,  $F$ -statistics, number of private (unique) alleles, migrants per generation, Nei's standard genetic distance, the Mantel test, and probability of identity. Structure 2.3 (Pritchard et al. 2000; Hubisz et al. 2009) was used for assignment tests. Cervus 3.0 (Marshall et al. 1998) was used to identify possible null alleles. A 1-tailed Fisher's exact test was used to determine whether males were more likely than females to exhibit allelic combinations typical of sites other than the one at which the individual was found (Conover 1999; Zar 1974) and was performed using SAS 8.2 (SAS 2001). To detect an overall level of significance of  $P \leq 0.05$ , a Bonferroni adjustment was made whenever multiple independent tests were used (Rice 1989).

Tests for linkage disequilibrium were completed on data for the geographic scales of the local trapping grids in southwestern Tennessee and the transcontinental regions and sequential Bonferroni adjustments (Rice 1989) were applied. Because of possible linkage disequilibrium, locus G10C was excluded from the remainder of the genetic analyses. For the remaining loci, less than 30% of the combinations of any 1 locus with the other loci across the different populations at any geographic scale showed significant linkage disequilibrium, and, so, it was inferred as unlikely that they were physically linked. In addition, locus G10B was identified as potentially displaying >5% null alleles. This locus was not used in the AMOVA for determining F-statistics, which are particularly sensitive to the inclusion of null alleles.

$H_o$  is the proportion of heterozygotes observed in the population and  $H_e$  is the proportion of heterozygotes expected in the population under the assumptions of HWE based on observed allelic counts. Tests for conformity to HWE were completed at each geographic scale and using only the set of regions for the transcontinental scale. At each scale, an exact test was applied (Weir 1996) to reveal deviations from expected values under the null hypothesis of random union of gametes, and a global test was applied to test for heterozygote deficiency across each site for all loci combined, each locus for all sites combined, and all sites and loci combined. Fixation indices (Wright 1943) or  $F$ -statistics were calculated with 999 permutations and missing values interpolated.

Number of migrants per generation ( $Nm$ ) was calculated as  $Nm = [(1 / F_{ST}) - 1] / 4$ .

Because of the desirable properties of the methods of Nei's (1987) standard genetic distances ( $D_s$ ) in contiguous populations (Weir 1996, Paetkau et al. 1997), these measures were calculated for all pairs of sites. The geographic coordinates for the center point of

the grid, county, or city was used for any specimen taken from a trapping grid or from an unknown location within a known county or city, respectively. Geographic coordinates for more accurately known locations of specimens were used when possible. Mean coordinates for all specimens within a site were averaged to produce the coordinates used in calculating geographic distances between sites. Nei genetic distance matrices were log-transformed to use with the geographic distance matrices in the Mantel test for IBD to indicate if gene flow across the landscape was uniform (Weir 1996; Paetkau et al. 1997). The Mantel test was performed with 9999 permutations. This produced a coefficient of correlation ( $R^2$ ) between genetic and geographic distance with a range from -1 to +1 and a test for a significant relationship. The null hypothesis of no significant relationship would be supported if random associations (permutation) between the genetic and geographic distances of the data set produced a similar correlation to the observed value. The prediction of a significant relationship would be supported if the observed correlation was closer to 1 or -1 than at least 5% of the random permutations (Nicola S. Flanagan, A Guide to GenAlEx6 Genetic Analysis in Excel, <http://www.anu.edu.au/BoZo/GenAlEx/>).

The program *Structure* 2.3 (Pritchard et al. 2000) was used to: 1) identify animals likely to be immigrants or to have an immigrant in their recent ancestry and their probable areas of origin (Paetkau et al. 1997); 2) identify possible population boundaries across which minimal gene flow occurs; and 3) determine whether 1 sex was more likely than the other to disperse among sites. The program *Structure* implemented Bayesian clustering algorithms using multilocus genotypes of sampled individuals to infer population structure and assign individuals to populations. A model was assumed for K

(possibly unknown) populations, each differentiated by a set of allele frequencies at each locus. Each individual was assigned by probability to 1 population or to more than 1 population if it was admixed, depending on whether its combination of alleles was typical of 1 or more than 1 of the populations, respectively. Each genetic data set was analyzed using: (1) 5 iterations at each K value; (2) 100,000 burn-in steps and 100,000 Markov chain Monte Carlo (MCMC) repetitions after burn-in, and (3) the models for admixed ancestries and correlated allele frequencies, referencing sampling locations as prior information (Hubisz et al. 2009) and with lambda set to 1.0. The modal value of K that best fit the genetic data was determined by the method of Evanno et al. (2005). Because exploratory runs at the transcontinental and the southeastern area scale did not clearly provide a best value for K, apparently confounded by the multi-scale nature of the data, these data sets were reanalyzed after removing from them the large number of records from the grids in southwestern Tennessee.

## **RESULTS**

Genotypes for 441 individuals from the trapping grids in southwestern Tennessee, and 215 individuals from the other sampling sites were used in the analyses and revealed 6 - 35 alleles per locus over the 9 loci for a total of 133 alleles. The estimate, excluding locus G10C, of the average probability that 2 randomly selected individuals from the same randomly breeding population had the same multilocus genotype (Probability of Identity, PI) for the entire sampling area spanning the United States and Canada was 2.318E-8 (1 in 43,137,335). The same estimate for the trapping grids in southwestern

Tennessee was 6.8382E-08 (1 in 14,623,609). For the same 2 scales, respectively, the estimates of the average probability of any 2 randomly selected individuals from the entire sample having the same multilocus genotype ( $PI \times$  population size) were 1.5207E-05 and 3.0157E-05.

*Observed and expected heterozygosity and HWE tests.*—At the scale of the southeastern area,  $H_o < H_e$  in 4 of 9 cases (44.4%) for each population with all loci combined, and in 4 of 8 cases (50.0%) for each locus with all populations combined. At the other geographic scales,  $H_o$  was  $< H_e$  for 70-100% of such comparisons. For the grand mean of all populations and loci combined,  $H_o$  was  $< H_e$  at each geographic scale. These grand means (and SE) for  $H_o$  and  $H_e$  were: 0.511 (0.042) and 0.555 (0.040) for transcontinental regions; 0.513 (0.031) and 0.542 (0.026) for transcontinental states; 0.515 (0.039) and 0.532(0.034) for sites in the southeastern area; and 0.526 (0.038) and 0.565 (0.041) for grids in southwestern Tennessee.

For the transcontinental regions, exact tests for each locus in each population showed that 5 of the 48 combinations (10.4%) deviated significantly from expected values for HWE after Bonferroni adjustment for table-wide  $P \leq 0.05$  ( $0.05/48 = 0.001$ ). After the Bonferroni adjustment, 4 of 6 sites (75.0%) showed significant ( $P \leq 0.00833$ ) heterozygote deficits with 8 loci included and 4 of 8 loci (50.0%) showed significant ( $P \leq 0.00625$ ) heterozygote deficits with all sites included. For the sites in the southeastern area, after a Bonferroni adjustment, exact tests for each locus in each population showed that 3 of the 72 combinations (4.2%) deviated significantly from expected values for HWE, 2 of 9 sites (22.2%) showed significant ( $P \leq 0.0056$ ) heterozygote deficits with 8 loci included, and 3 of 8 loci (37.5%) showed significant ( $P \leq 0.00625$ ) heterozygote



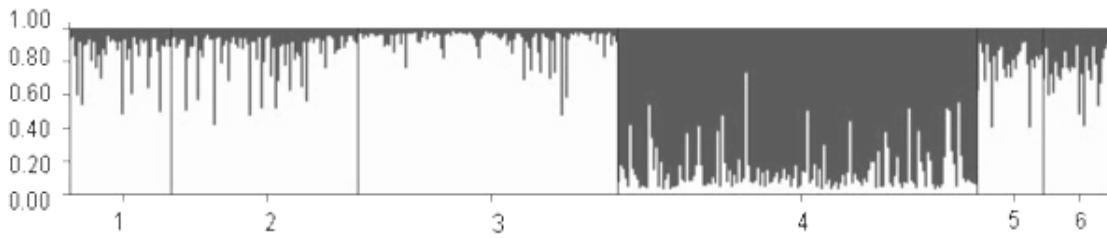
deficits with all sites included. For the grids in southwestern Tennessee, exact tests for each locus in each grid showed that 10 of the 48 combinations (20.8%) deviated significantly from expected values for HWE after Bonferroni adjustment; 5 of 6 sites (83.3%) showed significant ( $P \leq 0.00833$ ) heterozygote deficits with 8 loci included, and 2 of 8 loci (25.0%) showed significant ( $P \leq 0.0056$ ) heterozygote deficits with all sites included. For each of these 3 geographic scales, a highly significant heterozygote deficit existed for all loci and all sites together ( $P = 0.0000$ ;  $SE = 0.0000$ ).

*Mantel test for isolation by distance.*—For the test for IBD in genetic features, the Mantel probability was significant at all 3 scales: transcontinental regions; sites in the southeastern area; and grids in southwestern Tennessee ( $P = 0.049, 0.010, \text{ and } 0.023$ ; with Mantel correlation coefficient  $R_{xy} = 0.8140, 0.5230, \text{ and } 0.4652$ , respectively). However, for the largest and smallest of these scales, outlier data for the Northwest (Oregon) and Meeman, respectively—which were isolated from the remaining sites of those scales by much greater distances or major geographic barriers to raccoon migration—appeared to greatly influence the correlation. When data for these two sites were excluded, the correlations did not differ significantly from 0 ( $P = 0.343 \text{ and } 0.105$ , with  $R_{xy} = 0.2488 \text{ and } 0.4151$ , respectively), corresponding to the null hypothesis of no significant relationship.

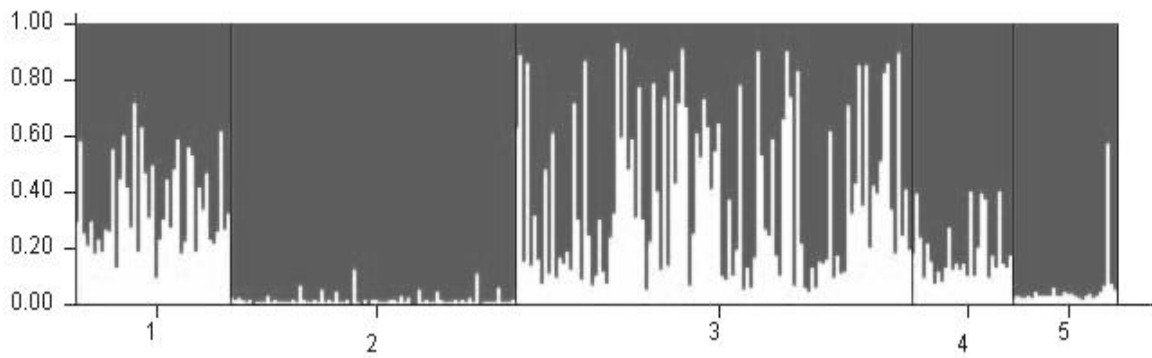
*Assignment test.*—The most probable genetic clusters identified by program *Structure* at each geographic scale are shown in Fig. 2. An individual represented by a vertical bar almost entirely, or about 50% or 25% of the shade of a cluster representative of a site other than that on which it was located, was likely to be an immigrant or have 1 immigrant parent or grandparent, respectively, from that other site.

**FIG. 2.**—Most probable genetic clusters, identified by program *Structure*, for individual raccoons (*Procyon lotor*) from sites at different geographic scales in the United States and Canada. Continued on next page.

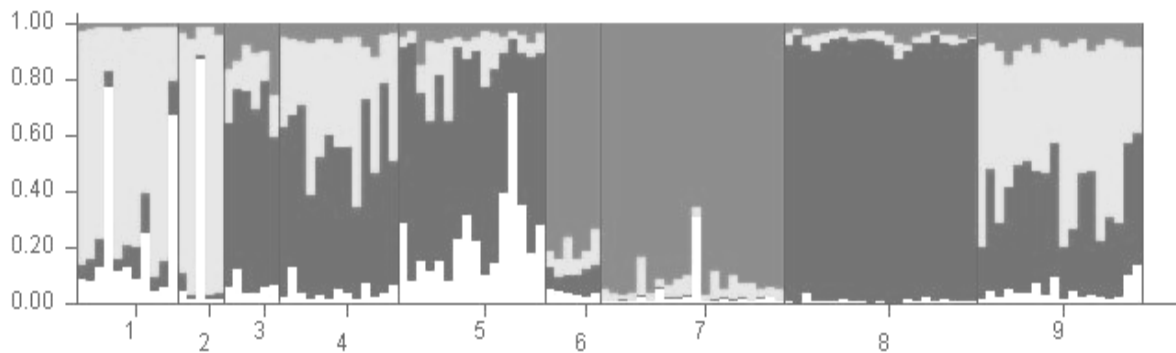
a)



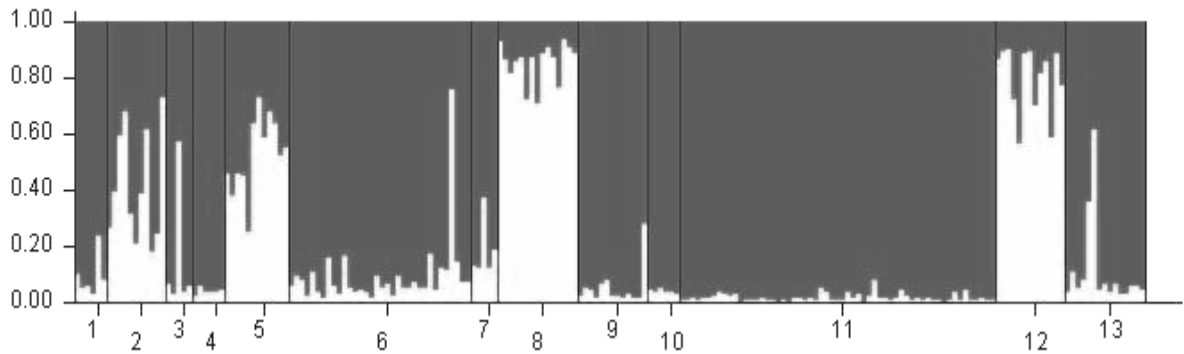
b)



c)



d)



**FIG. 2.**—Most probable genetic clusters, identified by program *Structure*, for individual raccoons (*Procyon lotor*) from sites at different geographic scales in the United States and Canada, continued from previous page. Within each graph, individuals are grouped by their locations. Each shade represents the genetic pattern typical of a particular cluster, and each narrow vertical bar represents a single individual and the proportions of its genotype representative of each of the genetic clusters. Modal number of clusters ( $K$ ) identified is 2 at each scale except  $K=4$  for the southeastern area. See text for abbreviations for the sites, and explanations. a) Grids in southwestern Tennessee; populations 1-6 were AC, D, H, M, MC, and P, respectively. b) Grids in southwestern Tennessee (Ames) without Meeman; populations 1-5 are AC, D, H, MC, and P, respectively. c) Sites in the southeastern area; populations 1-9 are AR, GA, IN, KYE, KYW, SC, TNNE, TNW, and TNSW, respectively. In this graph, white represents a cluster that did not dominate any of the sampled populations of the southeastern area. d) Transcontinental states after the removal of the samples from Oregon; populations 1-13 are AL, AR, GA, IN, KS, KY, LA, MB, NYVT, SC, TN, TX, and WI, respectively.

The genotypes of the raccoons from grids in southwestern Tennessee divided into 2 clusters—1 corresponding to the grid at Meeman and 1 corresponding to the 5 grids at Ames (Fig. 2a). Nearly all of these raccoons showed a small amount of admixture with the genetic pattern of the site at which they were not captured. No raccoons sampled from 1 site had genetics almost entirely consistent with having originated from the genetic cluster that was characteristic of the other. However, though these 2 sites were separated by some 75 km, 19 of 441 of raccoons (4.3%) showed admixture of near 50%, which was consistent with having 1 parent immigrating from the genetic cluster typical of the other site. These comprised 7 (4.6%) of the 152 raccoons captured at Meeman, of which 6 (85.7%) were males and 1 (16.7%) was female; and 12 (4.2%) of the 289 captured at Ames, of which 9 (75%) were males, 2 (16.7%) were females, and one had no recorded sex. A 1-tailed Fisher's exact test did not indicate that males were more likely to exhibit such admixture than females ( $\chi^2_1 = 2.6591$ ;  $P = 0.0795$ ). In addition, other individuals displayed at least 25% admixture with the genetic pattern typical of the cluster in which they were not located, indicating the likelihood of 1 grandparent immigrating from the opposite cluster.

Reanalysis of the data excluding the outlying grid at Meeman again revealed 2 clusters (Fig. 2b). The grids at Dusco Place and Pattersonville, which were separated from the other grids by the narrow North Fork of the Wolf River and a minimum of 3 km, revealed all individuals having genetics reflecting almost purely 1 cluster except for 1 male in Pattersonville. This reanalysis also showed individuals from Afternoon Course and Hancock Place to be highly admixed, and Morning Course to have genetics more reflective of the cluster of Dusco Place and Pattersonville.

For the sites of the southeastern area (Fig. 2c), northeastern Tennessee clustered strongly with South Carolina but only slightly with the much nearer eastern Kentucky or any other site. The site in northwestern Tennessee, separated from other nearby sites except that in southwestern Tennessee by the Mississippi or Tennessee Rivers, was the least admixed site for another genetic cluster, which was represented in decreasing amounts in Indiana and Kentucky, southwestern Tennessee, and the remaining sites, respectively. A 3<sup>rd</sup> cluster was represented in the highest proportions (least admixture) in Arkansas and Georgia, and then in decreasing proportions in the order of southwestern Tennessee, eastern Kentucky, western Kentucky, and Indiana. This appeared to be concentrated in the southern sites of the area. A 4<sup>th</sup> cluster did not dominate any sampled population but was most heavily represented in several of the most northwesterly sites-- Arkansas, Indiana, western Kentucky, and southwestern Tennessee. Heavily admixed sites included Indiana, eastern Kentucky, western Kentucky, and southwestern Tennessee.

For samples from the transcontinental states, the modal number of clusters, K, was 2. Samples from Oregon comprised 1 cluster and those from the remaining states comprised the other. Only minute admixture of the genetic pattern in Oregon was revealed at decreasing levels in Texas and Tennessee, followed by the others with virtually none. No migration of any recent ancestors of the sampled raccoons appears to have occurred between Oregon and the other transcontinental states. Reanalysis of the data after excluding the outlying site in Oregon again revealed 2 clusters. A genetic cluster comprised the following states with very little admixture except 1 migrant in some populations: Alabama, Georgia, Indiana, Kentucky, New York-Vermont, South Carolina,

Tennessee, and Wisconsin. The other cluster comprised with less than ¼ admixture: Manitoba and Texas. The remainder of the populations (Arkansas and Kansas) was mostly admixed between the 2 clusters. Thus, the 2 clusters roughly comprised the populations east of the Mississippi with low admixture vs. the populations west of the Mississippi with low to high admixture with the most highly admixed being those nearest the major and centrally located sampling sites east of the Mississippi.

The genetic distance between raccoons from Georgia and South Carolina was higher than geographic distance would suggest. The *Structure* analysis showed that 4 of the 5 raccoons from Georgia clustered with little admixture with the other populations that were east of the Mississippi. However, the 5<sup>th</sup> raccoon from Georgia may have increased the genetic distance with South Carolina. That raccoon had admixed genetics typical of the cluster represented in the sampled states that were west of the Mississippi River and more than 1200 km distant from the site in Georgia. Only 2 other raccoons had genetics similar to this, but, were distant from the sampled sites west of the Mississippi. The 1<sup>st</sup> of these 2 raccoons was from southwestern Kentucky, more than 730 km away from these sites across the Mississippi and Tennessee Rivers, and the 2<sup>nd</sup> was from Wisconsin, more than 860 km away from these sites. These 3 comprise 1.4% of the 215 individuals assigned to genetic clusters at the transcontinental state level. Of these 3 raccoons, 2 including the 1 from Georgia, were females.

*F-statistics.*—For each locus at each population, 68.9%, 55.5%, and 70.8% of  $F_{IS}$  combinations had positive values at the scales of transcontinental regions, sites in the southeastern area, and grids in southwestern Tennessee, respectively. For the combined populations for each locus at the same 3 scales,  $F_{IS}$  values were positive in 5 of 7

(71.4%), 3 of 7 (42.8%), and 6 of 7 (85.7%) of the cases (Table 1). For these data sets, 7 of 7 (100%), 6 of 7 (85.7%), and 6 of 7 (85.7%), respectively, of  $F_{IT}$  values were positive, and all F-statistics at each scale across all populations and loci pooled were positive and significantly different than 0 (Table 1).

Numbers of significant pairwise population  $F_{ST}$  values (and significance level after the Bonferroni adjustment) were 15 of 15 (0.0033) for the transcontinental regions, 13 of 36 (0.0014) for sites in the southeastern area, and 10 of 15 (0.0033) for grids in southwestern Tennessee (Table 2). Meeman was significantly differentiated from all the other grids in southwestern Tennessee. The westernmost grids at Ames (Dusco Place and Pattersonville) were not significantly differentiated from one another nor were the easternmost grids (at Hancock Place, Afternoon Course, and Morning Course). However, despite a maximum distance of only about 12 km among the grids at Ames, Dusco Place, which was the furthest westward of these grids was significantly differentiated from all 3 of the eastern grids, and Pattersonville, which was the 2<sup>nd</sup> furthest westward, was differentiated from 1 of the eastern grids

*Number of migrants per generation.*—Between the Northwest and any of the remaining transcontinental regions,  $N_m$  values were generally an order of magnitude lower than those among the regions excluding the Northwest. The highest  $N_m$  values at this scale were those between East Central and other regions excluding the Northwest. These  $N_m$  values were all above 10.0 while those among the remaining regions excluding the Northwest and East Central were all below 10.0, with the minimum being 5.572 between the Northeast and Southern Midwest. At the scale of the southeastern area, the highest  $N_m$  was between northwestern Tennessee and southwestern Tennessee (14.567),

**TABLE 1.**—F-Statistics and number of migrants per generation (Nm) for raccoons (*Procyon lotor*) determined as part of a study of genetic structure of microsatellite loci at local to transcontinental scales across the United States and Canada. F-Statistics and Nm at each microsatellite locus are over all sites over all transcontinental regions (A), sites in the southeastern area (B), and local trapping grids at the Meeman Biological Station and the Ames Plantation in southwestern Tennessee (C). F-statistics and probability values for all populations and loci were also pooled for each of these data sets. *P* is the probability, based on permutation across the full data set, that the actual data set has lower values than randomly selected sets for  $F_{ST}$ ,  $F_{IS}$ , and  $F_{IT}$ .  $F_{ST}$  is the degree of genetic differentiation among the subpopulations within the population.  $F_{IS}$  and  $F_{IT}$  are, respectively, departure from expectations for random mating for individuals within a subpopulation and such a departure for all of the individuals for the entire population.

Locus	$F_{IS}$			$F_{IT}$			$F_{ST}$			Nm		
	A	B	C	A	B	C	A	B	C	A	B	C
G10X	-0.049	-0.108	-0.110	0.402	-0.002	-0.093	0.429	0.096	0.015	0.332	2.364	16.365
PFL9	-0.008	-0.060	0.030	0.114	0.008	0.047	0.121	0.064	0.017	1.823	3.687	14.108
PL35	0.082	-0.007	0.048	0.151	0.116	0.080	0.075	0.122	0.033	3.067	1.802	7.293
PL40	0.058	0.078	0.043	0.276	0.150	0.053	0.232	0.078	0.011	0.829	2.940	22.815
PFL11	0.046	-0.061	0.026	0.122	0.033	0.047	0.080	0.089	0.022	2.891	2.546	11.170
PFL4	0.126	0.103	0.234	0.178	0.204	0.255	0.060	0.113	0.028	3.950	1.971	8.681
PL61	0.052	0.122	0.007	0.100	0.229	0.029	0.051	0.122	0.023	4.658	1.798	10.853
Mean	0.044	0.009	0.040	0.192	0.105	0.060	0.150	0.098	0.021	2.507	2.444	13.041
SE	0.022	0.035	0.038	0.041	0.036	0.039	0.052	0.008	0.003	0.601	0.261	2.000
Pooled	0.074	0.029	0.017	0.073	0.068	0.068	0.141	0.095	0.084			
<i>P</i>	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001			



**TABLE 2.**—Pairwise degree of genetic differentiation between subpopulations within the overall population ( $F_{ST}$ ) for microsatellite loci of raccoons (*Procyon lotor*) determined as part of a study of genetic structure at local to transcontinental scales across the United States and Canada.  $F_{ST}$  values are given below the diagonals and probability values based on 999 permutations are given above the diagonals of the tables. The “\*” probability values were significantly different from 0 at  $P \leq 0.05$  after the Bonferroni adjustment for Type 1 error for transcontinental regions (a), sites in the southeastern area (b), and local trapping grids at the Meeman Biological Station and the Ames Plantation in southwestern Tennessee (c). See text for abbreviations for the sites, and explanations.

a)

	EC	NE	NMW	NW	SE	SMW	
EC	--	0.001*	0.001*	0.001*	0.001*	0.001*	EC
NE	0.02	--	0.001*	0.001*	0.002*	0.002*	NE
NMW	0.02	0.032	--	0.001*	0.002*	0.001*	NMW
NW	0.28	0.332	0.317	--	0.001*	0.001*	NW
SE	0.03	0.038	0.026	0.353	--	0.001*	SE
SMW	0.02	0.034	0.022	0.257	0.042	--	SMW

b)

	AR	GA	IN	KYE	KYW	SC	TNNE	TNNW	TNSW	
AR	--	0.184	0.032	0.019	0.001*	0.002	0.001*	0.002	0.004	AR
GA	0.017	--	0.006	0.002	0.001*	0.068	0.001*	0.001*	0.003	GA
IN	0.043	0.082	--	0.008	0.003	0.010	0.001*	0.004	0.047	IN
KYE	0.030	0.068	0.042	--	0.003	0.001*	0.001*	0.016	0.013	KYE
KYW	0.051	0.102	0.055	0.025	--	0.011	0.002	0.057	0.001*	KYW
SC	0.079	0.045	0.059	0.068	0.045	--	0.086	0.004	0.001*	SC
TNNE	0.070	0.084	0.045	0.045	0.023	0.016	--	0.001*	0.001*	TNNE
TNNW	0.053	0.095	0.044	0.017	0.010	0.052	0.032	--	0.001*	TNNW
TNSW	0.026	0.064	0.020	0.013	0.026	0.044	0.037	0.021	--	TNSW

c)

	AC	D	H	M	MC	P	
AC	--	0.001*	0.001*	0.001*	0.126	0.001*	AC
D	0.011	--	0.001*	0.001*	0.002*	0.011	D
H	0.009	0.012	--	0.001*	0.009	0.101	H
M	0.019	0.021	0.027	--	0.001*	0.001*	M
MC	0.005	0.016	0.011	0.016	--	0.020	MC
P	0.021	0.010	0.004	0.016	0.012	--	P

followed by those between a site in western Tennessee and a site in Kentucky. The lowest Nm values at this scale were between a site in Kentucky or northern Tennessee and one of the southernmost states and between Arkansas and South Carolina, between Georgia and Indiana (lowest, at 2.418), and between Georgia and South Carolina (also very low, at 2.784). At the scale of the grids in southwestern Tennessee, the highest Nm values were between Hancock Place and Dusco Place and between Hancock Place and Pattersonville (highest at 30.940). Lower Nm values at this scale were between pairs of grids at Ames including 1 of the easternmost and 1 of the westernmost grids with the lowest being between Morning Course and Pattersonville (11.441). These Nm values were lower on average than the values between the much more distant Meeman and a grid at Ames. Values of Nm are given in Hisey (2012), Appendix III.

## DISCUSSION

The prediction of an effect of IBD (Wright 1943) was supported but only weakly at some geographic scales examined because of irregularities that may have been influenced by landscape barriers or corridors and instances of long-distance dispersal. The prediction that migrants among sites at each scale would be predominantly males was not strongly supported though more males than females appear to have dispersed at most scales.

*Heterozygosity and HWE tests.*—At each geographic scale, the number of observed heterozygotes were lower, and significantly different, than the expected number of heterozygotes under HWE for all combined loci and populations. The same was true for multiple cases when examining each locus at each population, each locus across

combined populations, and each population across combined loci. Near Chicago, Illinois, and across the western and central United States, respectively, the microsatellite DNA (Ary 2003) and allozymes (Hamilton and Kennedy 1987) of raccoons similarly exhibited heterozygote deficits and departure from the expectations of HWE. These were ascribed to the Wahlund effect (Wahlund 1928) of inclusion of substructured populations within a single sample (Ary 2003; Hamilton and Kennedy 1987) and immigration or emigration at each site (Ary 2003). In Ontario and New York, the microsatellite DNA of raccoons displayed a heterozygote deficit and deviation from the expectations of HWE in only 1 locus in 1 of 2 sites, and this was eliminated by subdividing that site (Cullingham et al. 2009). Microsatellite DNA of mink from 1 site in Tennessee and 7 sites in Arkansas revealed several loci that did not meet the expectations of HWE at some locations but did meet these expectations with all sites and loci combined (Stevens et al. 2005).

Modeling with the program *Structure* in the current study revealed substantial genetic admixture occurring among many of the sampling sites at all scales, and that genetic clustering occurred even at local levels. Therefore, the location of a sampling site often did not correspond exclusively to that of a genetic cluster, and substructuring occurred in many sampling sites, which can lead to significant heterozygote deficiencies because of the Wahlund effect (Wahlund 1928). Such substructure at local scales might be due to multiple lineages of highly related raccoons in spatial clumps that are genetically differentiated from one another (Chesser 1991a, b; Sugg et al. 1996; Hisey 2012). This high level of heterozygote deficit was found in most of the grids in southwestern Tennessee across all loci.

*Mantel test for isolation by distance.*—IBD (Wright 1943) was evident at all three scales in the current study, but the significance of this trend was primarily due to 1 population at some scales. Microsatellite DNA of Eurasian badgers revealed IBD at local to transcontinental scales, implying few barriers to dispersal (Pope et al. 2006). High vagility characterizes most carnivores (Paetkau 1995; Serfass et al. 1998; Kyle and Strobeck 2002) including raccoons, in which males are usually the predominant dispersers (Kaufmann 1982; Tabatabai 1988). Movements may be due to searches for food, escape from seasonal flooding of bottomlands, drying of ephemeral streams, searching for mates, and juvenile dispersal (Greenwood 1980; Sandell 1989; Kaufmann 1982). High levels of gene flow might be expected for raccoons if mating occurs far from the natal area, with very few barriers inducing irregularities. If so, genetic similarity would decline purely and only gradually on the basis of increasing distance.

At the local and transcontinental scales in the current study, significant IBD effects were mostly due to the influence of the outlying sites at Meeman and the Northwest (Oregon), which were isolated from the remaining sites of that scale by much greater distances or major geographic barriers to raccoon migration. Omission of the data of the outlying site for these two scales resulted in lack of a significant IBD effect at each, possibly because of anomalies like genetic clustering and long-distance migration. At the local scale of grids in southwestern Tennessee, data from Carver (2009) based on direct observations revealed only 3 raccoons changing grids (Carver 2009). However, many raccoons might have dispersed over the distance between grids at Ames as reflected by the low IBD correlation and other genetic analyses in the current study, and similar dispersal distances in other raccoon studies (Cullingham et al. 2008b; Rosatte et al. 2007,

2010). When only data from Ames were used, a slight effect of IBD was still observed though centers of grids were only about 3.5 to 12 km apart, possibly because of different lineages partitioning to different grids as discussed in the following paragraphs. However, the correlation was low and not statistically significant ( $R_{xy} = 0.415$ ;  $P = 0.105$ ).

No significant relationship between geographic and genetic distance was found for raccoons at sites separated by 25-50 km near Chicago, Illinois (Ary 2003), with the same microsatellite markers used in the present study, or for mink in Arkansas and Tennessee (Stevens et al. 2005). Investigations of genetic variation for the raccoon over its geographic range using starch gel protein electrophoresis found little genetic structuring among sites in the southeastern United States (Beck and Kennedy 1980; Dew and Kennedy 1980), but significant differences between this and other regions (Hamilton and Kennedy 1987). However, microsatellites have proven useful in more finely distinguishing this spatial structuring of genetic variability for species in which little such structure was found using allozymes (Ciski et al. 2003; Paetkau et al. 1995). In some cases, genetic structuring indicative of long term isolation of nearby or adjacent populations have been discerned in microsatellite studies of large carnivores like eastern black bears that have the potential to range widely (Ciski et al. 2003; Paetkau et al. 1997).

*Assignment tests.*—These analyses revealed both boundaries of genetic clusters that may indicate barriers to raccoon migration and long-distance dispersers among these clusters. The clusters indicated negligible admixture between Oregon and the site of any other sampled state via migration of recent ancestors (Pritchard et al. 2000) including that by long-range transport by humans such as was known elsewhere (Cullingham et al.

2008a; Dew and Kennedy 1980; Hamilton and Kennedy 1984; Rosatte et al. 2007). This was consistent with other findings on the genetics of raccoons (Hamilton and Kennedy 1987) and the historical lack of raccoons in the intermontane west (Lotze and Anderson 1979). After the omission of Oregon from the further analyses, the sampled states nearest to the Mississippi River but on its west side showed substantial genetic characteristics typical of both the less admixed cluster in the states further to the west and the only slightly admixed genetic cluster on the east side of the river. The river appeared to be only a partial barrier and the land to its west that was more xeric, less forested and generally less hospitable to raccoons (Kaufmann 1982; Baldwin 2003; Baldwin et al. 2006) may have further filtered their movements. The Mississippi River appears to have blocked gene flow of some species (Soltis et al. 2006), and broad, rapid rivers may hinder movements of the raccoon as well (Cullingham et al. 2009; Smith et al. 2002) though it is a competent swimmer (Gehrt 2003). Little is known about the extent to which habitat preferences of the raccoon may affect spatial patterns of gene flow and resulting genetic variation over most of its range (but see Cullingham et al. 2008a, b; 2009). Some studies report raccoons associating with particular habitat variables (Wilson 1996; Baldwin 2003; Baldwin et al. 2006), with highest abundance in bottomland forests, along riparian corridors, and in other wetland habitats, and movements of individuals rarely if ever extending into areas away from watercourses (Kaufmann 1982). However, raccoons are usually considered habitat generalists that are successful in human-altered habitats such as urban areas (Tabatabai 1988) and crop fields (Chamberlain et al. 2007; Beasley et al. 2007a, b) and are capable of crossing nearly every type of terrestrial community (Gehrt 2003; Kaufmann 1982).

Of the 3 raccoons from eastern Georgia, western Kentucky, and eastern Wisconsin that displayed admixed genetics typical of 1 parent originating from the cluster of sampled states to the west of the Mississippi River, 2 including that from Georgia were females. Transport by humans, which may have occurred with these 3, has occurred in other parts of the raccoon's range (Cullingham et al. 2008 a, b; Dew and Kennedy 1980; Hamilton and Kennedy 1984; Rosatte et al. 2007), and may not be as subject to male bias as is natural dispersal among mammals. For sites in the southeastern area, a cluster that was not dominating any sampled population was found in Arkansas, Indiana, western Kentucky, and southwestern Tennessee. This cluster may be characteristic of a population at the northwestern edge of the area, perhaps strongly represented in Missouri or Illinois, which was not directly sampled. A high proportion of the genetic pattern typical of this cluster was found in a single individual in each of Georgia and western Kentucky as also seen in the data of the transcontinental states.

Of 2165 cases of a raccoon being captured in 2-consecutive years in a study in Ontario, only 10 males, and 1 female were found to move as far as 40-45 km (Rosatte et al. 2010). Prior records note occasional movements in natural populations of 40-295 km for males and more than 20 km for females (Lynch 1967; Priedwert 1961; Tabatabai 1988). Raccoons have also been translocated long distances by humans (Cullingham et al. 2008a; Dew and Kennedy 1980; Hamilton and Kennedy 1984; Rosatte et al. 2007). Use of genetic markers provided more complete evidence of proportions of the population or immediate ancestors migrating longer distances than mark-recapture data alone in this and other studies, with the added advantage that sampling need only be conducted once (Cullingham et al. 2008b). Capture-recapture data alone detected no



raccoons switching between Meeman and Ames and only 3 (1.0%, all males) switching among grids at Ames: 6.402 km from Afternoon Course to Hancock Place in 82 days, 11.288 km from Dusco Place to Afternoon Course in 347 days, and 9.355 km from Morning Course to Dusco Place in 735 days. The assignment test indicated a high rate of dispersal between the genetic clusters typical of Ames and Meeman, with that by males predominating but not significantly greater than that by females. However, even the 3 females captured at Meeman or Ames but displaying about 50% admixed genetics from the cluster typical of the other site may have received them through an immigrant father. Spatial genetic autocorrelation and sibship analyses on the data set of the current study revealed 2 (8.7%) of 23 full brother pairs detected were separated by 6-10 km and 3 (13.0%) by 70-85 km but full sister pairs by no more than 2 km and dispersal of most females of < 800 m (Hisey 2012). Compared to other studies (Lynch 1967; Prierwert 1961; Rosatte et al. 2010; Tabatabai 1988), the present findings of 1 parent possessing genetics typical of a site 75 km away in 4.3%, and 730-1200 km away in 1.4% of sampled individuals revealed extremes in extension and proportions of dispersal by raccoons effectively assimilated into natural populations through reproduction. Dispersal distances estimated from distances between sites must be interpreted with caution because the boundary of a genetic cluster predominantly found at one sampling site or set of sites may fall anywhere between it and the neighboring set of sites. Yet, these estimates of proportions of long-distance dispersers must be considered minimums because only a minute proportion of sites that could have produced immigrants were actually sampled. Conversely, considering the general abundance of raccoons (Sanderson 1987), and the extent of movements found by prior studies despite limitations

on detectability (Lynch 1967; Priewert 1961; Rosatte et al. 2010; Tabatabai 1988), large numbers may be moving over long distances with the potential to carry diseases or colonize new areas.

*Fixation indices.*—In the current study, fixation indices generally increased with increasing distances among populations. These measures were higher at the smallest scales and lower at the larger scales than was anticipated from prior studies (Cullingham 2007; Hamilton and Kennedy 1987; Kyle and Strobeck 2002; Stevens et al. 2005), but consistent with multiple lineages of females on a site (Chesser 1983, 1991a, b; Sugg et al. 1996; Ratneyeke et al. 2002) and high rates of male dispersal (Gehrt and Fritzell 1998; Greenwood 1980; Ratneyeke et al. 2002). Some sites separated by geographic barriers had unusually high  $F_{ST}$  values.

The  $F_{IS}$  and  $F_{IT}$  (Wright 1943) for all populations and loci combined were positive and significantly different from 0 at each geographic scale. Such inbreeding coefficients that were higher than expected for randomly breeding populations were probably due to the Wahlund effect from sampling multiple genetic clusters as 1 subpopulation or population (Wahlund 1928) as noted for the tests of HWE. At the local scale of grids, such clusters may have comprised lineages of closely related females and their young (Chesser 1983, 1991a, b; Sugg et al. 1996; Ratneyeke et al. 2002).

$F_{ST}$  values significantly greater than zero indicate genetic differentiation among sites (Chesser 1991a; Wright 1943). Low but significant ( $F_{ST} < 0.05$ ,  $p < 0.05$ ) values were expected among the sites of the southeastern area while values among the local sites were not expected to be significant. These expectations were based on patterns found in microsatellite analyses of both semi-aquatic (Stevens et al. 2005) and terrestrial (Kyle

and Strobeck 2002) mid-sized carnivores, and studies of allozymes and mtDNA of raccoons (Cullingham 2007; Hamilton and Kennedy 1987). However, an analysis of raccoons near Chicago, Illinois using the same microsatellite markers used in the present study found moderately to highly significant  $F_{ST}$  values between pairs of sites separated by only 25-50 km (Ary 2003). Most of the  $F_{ST}$  values in the southeastern area in the current study were consistent with the previously stated expectations ( $<0.05$ ), but those values for pairs of sites that included Arkansas or Georgia were frequently higher. The inclusion in the sample from Georgia of the genetics of the long-distance migrant, and the separation of the raccoons in Arkansas from the others by a major river may explain the greater genetic differentiation (Cullingham et al. 2009; Smith et al. 2002; Soltis et al. 2006). Also, contrary to the expectations stated previously, the  $F_{ST}$  values for only 13 of 36 pairs of sites in the southeastern area were significantly different from 0, and these were mostly for pairs including a peripheral site such as Arkansas, Georgia, Indiana, or South Carolina. The genetic differentiation among the other sites may have been reduced by high rates of dispersal (Lynch 1967; Piewert 1961; Tabatabai 1988) or transport by humans (Cullingham et al. 2008a; Dew and Kennedy 1980; Hamilton and Kennedy 1984; Rosatte et al. 2007) noted for raccoons in the current and prior studies. An unanticipated result at the local scale was that 5 pairwise  $F_{ST}$  values out of 10 among the grids at Ames differed significantly from 0. Such significant genetic differentiation among nearby sites was likely influenced by limited female dispersal, which was suggested in other raccoon studies (Cullingham et al. 2008a; Gehrt and Fritzell 1998; Ratnayeke et al. 2002). This is consistent with the current mark-recapture data in which no females were detected as

having dispersed from 1 grid to another, and spatial genetic autocorrelation and parentage analyses that found females predominantly dispersing less than 800 m (Hisey 2012).

Allozymes revealed substantial genetic divergence of the Northwest from the eastern populations (Hamilton and Kennedy 1987). Likewise, in the current study, values of  $F_{ST}$  between the Northwest and any other region were much higher than those among the other regions (mean = 0.3078 vs. 0.0287, respectively). These concurring findings suggest additional investigation to determine whether the raccoons in the westernmost states are taxonomically different from other populations in North America or display a founder effect due to the immigration of a small group (Whitlock and Mccauley 1999).  $F_{ST}$  values between transcontinental regions generally increased with increased geographic distance, and all were all significantly different from 0.

*Number of migrants per generation.*— Nm values may be inaccurate because they are based on potentially unjustified assumptions including the ones stated above for the island model (Mills and Allendorf 1996). However, such values may be useful if they are in accord with other estimates of dispersal (Whitlock and Mccauley 1999). Nm values showed the highest gene flow between the Northwest and more easterly populations was with the southwestern-most sites. However, this gene flow was still very low compared to the substantial gene flow across the area from the east side of the Rocky Mountains to the Atlantic coast, including the Appalachian Mountains. Nm values for the Northwest paired with some of the other transcontinental regions were at a level (mean = 0.962) which may indicate that migration was sufficient to retain significant genetic diversity yet prevent extremely high divergence (as revealed by  $F_{ST}$ s) among populations (Mills and Allendorf 1996). Among all other regions, excluding the Northwest, Nm values were

about an order of magnitude higher (mean = 9.264) suggesting sufficient gene flow to counter drift, so that genetic divergence between some sites fell below the level of significance. Investigations of most species including solitary carnivores have expected and disclosed significant, if low, genetic differentiation within regional areas, which was sometimes explained as due to habitat preferences and restricted dispersal routes (Ciski et al. 2003; Kyle and Strobeck 2002; Paetkau et al. 1997; Serfass et al. 1998; Stevens et al. 2005). The populations in the southeastern area in the current study exhibited values for  $N_m$  about an order of magnitude higher, and  $F_{ST}$  that were much lower than those for the mink from sites in Arkansas and Tennessee (Stevens 2002). The mink is a smaller solitary carnivore than the raccoon and is likely to have more limited dispersal (Stevens et al. 2005).

The raccoon's distribution currently is nearly continuous over the entire lower 48 states of the United States from southern Canada to Mexico but historically did not include the Rocky Mountains and the deserts of the southwestern United States (Lotze and Anderson 1979; Gehrt 2003). The only area of the raccoon's former geographic range connecting the populations of the Pacific coast with the other populations was a narrow band along the coast of southern California, though the separation at the northern edge of the distribution was only by a narrow gap in the Rockies between British Columbia and Alberta (Lotze and Anderson 1979). Findings of the current study suggest that the gap in the north indeed deterred gene flow and the connection in the south provided gene flow via the Southern Midwest (Texas). Though the geographic distance from Oregon to the nearest sampling sites on the eastern side of the Rocky Mountains decreased slightly in the order of Texas to Kansas to Manitoba, the pairwise  $N_m$  values

also decreased in the same order (1.295, 1.018, and 0.757, respectively, with the latter only 58.4% of the former). However, the Southwest still apparently presents a substantial barrier to gene flow, as the Nm between the Northwest and the Southern Midwest was much lower than the Nm between the latter and the Northeast (1.29 vs. 5.57, respectively) or other eastern populations from which it was similarly distant. Most of the sites sampled in the current study were historically connected by eastern deciduous forest (Raven et al. 2010). However, the prairies, mountains, and deserts further to the west, which support little of the lowland riparian forests that raccoons prefer (Kaufmann 1982; Baldwin 2003; Baldwin et al. 2006), isolated them from the Northwest and may act as barriers to their dispersal. Raccoons currently inhabiting areas once vegetated by prairie concentrate use in woodlots, agricultural fields, or near sources of water, which historically were very limited in extent or absent (Chamberlain et al. 2007; Beasley et al. 2007a, b). Raccoons have been reported to be translocated as pets or for hunting purposes (Dew and Kennedy 1980; Hamilton and Kennedy 1984), or stowed away in human transport (Cullingham et al. 2008a; Rosatte et al. 2007) among eastern and central populations. Apparently neither these types of movements nor the recent range expansion spanning the former gap in distribution between the eastern and western populations have reduced the historical effect on our findings of western raccoons differing more genetically from northern than southern populations east of the Rocky Mountains. Should raccoon rabies or another disease infect the populations on 1 side of the Rockies, this bottleneck in movement at the southern end of the Rockies may make efforts to control its spread most effective in that area. Narrowing landscapes are

proposed as effective zones to use for barriers in rabies control efforts (Cullingham et al. 2008a).

The epizootic of raccoon rabies had long been restricted to Florida and its neighboring states but was initiated in Virginia by raccoons transported for hunting and spread from there across the entire Atlantic seaboard as far as Canada in 20 years (Gehrt 2003). This became the greatest epizootic on record (Cullingham et al. 2009) including the sites incorporated in this study in South Carolina, Georgia, and New York-Vermont. Long-distance movements must be investigated and incorporated into models of the spread of disease, as such movements appear to pose real threats for extensions of the rabies epizootic elsewhere (Rosatte et al. 2007; Smith et al. 2002). Of great concern is the recent extension of this epizootic westward (Gehrt 2003), which may threaten the states to the west of the Appalachians where rabies has not been observed (Cullingham et al. 2008a). The substantial migration of animals shown by the current study between South Carolina, Georgia, or New York-Vermont, and the more westerly states excluding Oregon (Nm mean of 4.15; range of 1.80-12.05 vs. a mean of 5.86 and range of 2.01 - 21.48 among just the latter) could facilitate the spread of rabies (Coyne et al., 1989; Macdonald and Laurenson, 2006). This is consistent with the assignment test in the current study showing the genetics of the site in northeastern Tennessee clustering strongly (across the Appalachian Mountains) with those of the site in South Carolina. Patterns in mitochondrial DNA (Cullingham et al. 2008a) and allozymes (Beck and Kennedy 1980; Dew and Kennedy 1980) also suggest little isolation between the states of the southeastern Atlantic seaboard and others to their west.

Novel approaches in this study included the analysis in patterns of microsatellite DNA of raccoons at local to transcontinental scales, including states bordering the areas of the intermontane West that were formerly unoccupied by raccoons (Lotze and Anderson 1979). The fine resolving power and biparental inheritance of microsatellite DNA facilitated examination of the effects of movements and philopatry of both males and females. This approach permitted detection in natural populations of higher frequencies of dispersal and at longer distances than previously reported (Cullingham et al. 2008a; Lynch 1967; Piewert 1961; Rosatte et al. 2010; Tabatabai 1988), initial identification of an apparent corridor of migration in the Southwest, and blockage of migration by high mountains and unforested land in the West. Overall, the findings of the current study supported the prediction of an effect of IBD (Wright 1943) at each geographic scale, but after removal of outlying populations from the analysis at the transcontinental and local levels, the effect of IBD at these scales was no longer significant. Genetic differences were also amplified between sites spanning landscapes that likely represented barriers to raccoon dispersal, such as major rivers (Cullingham et al. 2009; Smith et al. 2002), the highest ranges of mountains, and unforested, xeric land (Baldwin 2003; Baldwin et al. 2006; Kaufmann 1982). Genetic differentiation among sites ( $F_{ST}$  values) in the present study generally increased with increasing distances among sites at all scales as anticipated from prior work (Hamilton and Kennedy 1987). In the present study, differentiation was similar at the local scale to that of microsatellites of raccoons elsewhere (Ary 2003). However, this differentiation was more frequently significant at the local scale and less frequently significant at the southeastern area scale than reported in microsatellites of other midsized carnivores (Kyle and Strobeck 2002;



Stevens et al. 2005) and studies of the allozymes and mtDNA of raccoons (Cullingham 2007; Hamilton and Kennedy 1987). The patterns in microsatellites were consistent with population subdivision (Ary 2003) such as multiple female lineages on local sites (Chesser 1983, 1991a, b; Sugg et al. 1996; Ratneyeke et al. 2002) and substantial long-range movements, respectively.

In addition, the analyses in the current study did not strongly support the prediction based on previous reports (Lynch 1967; Priewert 1961; Rosatte et al. 2010; Tabatabai 1988) that migrants among sites at each scale would be males. Though 15 males and 3 females at smaller scales (a total of 4.3% of all samples) displayed genetic similarity higher than 50% admixture with clusters typical of sites about 75 km distant from the site at which they were sampled, the difference between proportions of these males and females only approached significance. At the largest scale, 2 females and 1 male (1.4% of all raccoons sampled at this scale) had this level of admixture with clusters typical of sites 730-1200 km distant from the sites at which they were sampled. To better understand the relationships between behavioral, habitat, and genetic patterns, which are crucial to the management of this key species, responses of dispersal and lineage formation (Gehrt and Fritzell 1998; Ratneyeke 2002) to environmental effects must be clarified. In addition, intensive study of the factors investigated here is needed in other parts of the raccoon's range including western North America (Gehrt 2003).

## CONCLUSION

1. The current study of spatial-genetic patterns of raccoons was the most geographically extensive to date and employed microsatellite DNA to clarify the effects of movements of each sex at multiple geographic scales.
2. A clear effect of IBD was found at each geographic scale but was dominated by the effects of outlying populations at transcontinental and local scales and was no longer significant when they were removed.
3. Though genetic differentiation between sites generally increased with geographic distance, additional increases were found across areas that appeared to be barriers to raccoon movements such as major rivers, high mountains, and xeric unforested habitat.
4. A trend of males crossing population boundaries and females remaining on the sampling site at the smallest geographic scales appeared to contribute to the levels of genetic differentiation observed, but the difference between sexes was not significant. This weak trend of sex bias was possibly reversed at the largest geographic scales.
5. Migration of at least one parent (possibly aided by human transport) possessing genetics typical of sites 75-1200 km away was observed in 22 (3.4%) of the sampled cases. Such instances may produce a considerable effect on genetic patterning and threaten to extend the epizootic of raccoon rabies.
6. At many of the sites, and over all sites combined,  $F_{IS}$  and  $F_{IT}$  had positive values, and less heterozygosity was observed than expected under the assumptions of HWE. This was likely due to genetic substructuring within the boundaries of sites that did not closely correspond to the boundaries of genetic clusters.

7. The highest estimate of Nm between the Northwest and more easterly populations was with the southwestern-most site. However, this estimate was still very low compared to the substantial migration across the area from the east side of the Rocky Mountains to the Atlantic coast, including the Appalachian Mountains. The mountains and deserts of western North America may help block the spread of raccoon-borne diseases, especially if control measures are applied in the Southwest; but the Appalachians are unlikely to help block such diseases.
8. Intensive investigation of lineage effects and the factors addressed in the current study is needed in additional parts of the raccoon's range including the western mountains and deserts to better understand the relationships between behavioral, habitat and genetic patterns, which are crucial to the management of this key species.

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#### **CHAPTER IV: SPATIO-TEMPORAL DISPERSION OF KIN GROUPS OF THE RACCOON (*PROCYON LOTOR*)**

The formation of lineages of highly related individuals in close proximity can have powerful influences on the geographic patterns of genetics (Chesser 1991a, b; Sugg et al. 1996) and the development of sociality (Hamilton 1964; Greenwood 1980; Chesser 1991a; Sugg et al. 1996). Such formation of lineages can be affected by the balance between residency and dispersal (Waser and Jones 1983; Ratnayake et al. 2002; Handley and Perrin 2007). Among mammals, natal dispersal among males and philopatry (site fidelity to the natal home range) among females is the predominant pattern (Greenwood 1980; Waser and Jones 1983; Handley and Perrin 2007). This pattern can promote the formation of lineages of nearby, closely related females with characteristic microgeographic genetic structuring as has been discovered in semi-gregarious (van Staaden et al. 1994) and gregarious-mammalian species (Dobson et al. 1998, 2004; Long et al. 1998; Pope 1998). Male-biased dispersal also is the prevalent pattern in solitary mammals (Greenwood 1980; Waser and Jones 1983; Handley and Perrin 2007), which are much more numerous than their gregarious counterparts (Bekoff et al. 1984; Gittleman 1989). However, the magnitude of temporal and spatial dispersion of closely related individuals over varied habitats and environmental conditions have not been previously examined in solitary mammals or most other mammalian species. Extensive studies are needed to more clearly understand these patterns.

The raccoon (*Procyon lotor*) is an interesting model species for testing hypotheses regarding the extent of lineage formation in solitary mammals. At least for restricted periods of favorable environmental conditions and in preferred habitats, female raccoons have been found to remain on sites for multiple years and to display clustering of close

relatives suggestive of lineage formation in a solitary carnivore (Ratnayeke 1997; Gehrt and Fritzell 1998a, b; Ratnayeke et al. 2002). Such preferred habitats are lowland forests and near water sources (Kaufmann 1982; Baldwin 2003; Baldwin et al. 2006). However, raccoons live in wide variety of habitats (Lotze and Anderson 1979) and turn-over is high in most studies (Johnson 1970; Moore and Kennedy 1985; Stevens et al. 1995; Maris 1998). For both sexes, some adult raccoons exhibit strong site fidelity over multiple years, but the home ranges of others can shift over years (Tabatabai 1988; Sumners 1992; Sumners and Kennedy 1995; Gehrt 2003). Duration of site fidelity might be related to resources such as food (Ladine 1995; Gehrt 2003). Higher rates of long-term site fidelity might occur in favorable habitats and when resources are predictable between years but dispersal of raccoons might occur when resource availability changes (Gehrt 2003). Currently, the spatial and temporal extents of lineages in varied habitats and environmental conditions are unclear for solitary mammals including the raccoon.

*Procyon lotor* is a long-lived and highly mobile species (Haugen 1954; Gittleman 1986; Nowak 1991) and is among the largest of the carnivores that can be recaptured routinely enough for robust monitoring (Gehrt and Fritzell 1996). Determination of the extent of lineage formation in this species might provide insights into this characteristic in other solitary carnivores that also predominantly display female philopatry and male dispersal (Greenwood 1980; Waser and Jones 1983; Handley and Perrin 2007). The proportions of the populations of raccoons involved in dispersal and philopatry also are of special interest because of the effects on the speed of the extension of epidemics such as raccoon rabies, the largest epizootic on record (Cullingham et al. 2009). These proportions also influence the utility of removal of raccoons in efforts to reduce 1) the

spread of such disease, 2) predation on species of conservation concern (Garrott et al. 1993; Jennings et al. 2006), 3) conflicts with humans in urban areas, and 4) damage to crops (Gehrt 2003).

The objective of this study was to assess the temporal and spatial dispersion of closely related raccoons across varied habitats and environmental conditions in southwestern Tennessee. We tested the following two predictions. 1) The prevalent form of spatial dispersion of first order relatives across varied habitats and environmental conditions is in simultaneous multi-year clusters (Ratnayeke 1997; Gehrt and Fritzell 1998a, b; Ratnayeke et al. 2002). 2) Such spatial dispersion of kin is associated over multiple years with varying environmental conditions (Gehrt 2003). We used genealogical and spatial genetic autocorrelation analyses of raccoons sampled over 5-9 years on 6 trapping grids in southwestern Tennessee to assess these predictions. Also, we evaluated the distance of dispersion of male compared to female relatives and the prevalence of lineages that immigrated as a unit. The relationship of environmental conditions to the dispersion of kin is poorly understood for most mammals, and particularly for the solitary species. The current study provides novel insights on the demography and management of a key mammalian species.

**MATERIALS AND METHODS--*Study Area***--This investigation was performed on 6 live-trapping grids comprising a total of 370 trapping stations and 13.8 km<sup>2</sup> in southwestern Tennessee. These grids were at the Ames Plantation (hereafter termed Ames) in Fayette and Hardeman counties and 75 km northwest at The University of Memphis' Meeman Biological Station (hereafter termed Meeman), near Millington, Shelby Co. At Ames, 5

grids separated by a mean distance of 5.2 km (minimum 1.6 km) each comprised an 8 by 8 array of 64 traps spaced at about 230 m and covering 259 ha (Fig. 1). At Meeman, a single grid comprised a 5 by 10 array of 50 traps spaced at about 150 m and covering 81 ha (Ladine 1995, 1997). Raccoon-sized Havahart (Woodstream Corporation, Lititz, Pennsylvania) or Tomahawk (Tomahawk Live Trap Co., Tomahawk, Wisconsin) live traps were used. Habitat on the grids included upland and bottomland forests, crops, oldfields, kudzu, permanent and intermittent ponds and streams, and adjacent to 3 of the grids at Ames, the North Fork of the Wolf River (Ladine 1995, 1997; Baldwin 2003; Carver 2009). From archives at the National Climate Data Center (NCDC, Asheville, North Carolina) we obtained annual data on precipitation that were originally recorded from the weather station at the Memphis International Airport.

*Trapping procedures*--Each mark-recapture trapping session comprised about 2000 trap nights (1 trap night = 1 trap set for 1 night). Sessions at Meeman comprised 40 selected days spanning the winter breeding season each year for 1991-2006 and 2008-2009 and spanning the summer rearing seasons of 2001-2003. Sessions at Ames comprised 32 selected days spanning the winter breeding season each year from fall 2000 to Spring 2005 and the summer rearing season from 2001-2003. We conducted sessions on each of the 5 grids during each winter, on 2 of the grids during each summer, and on 1 of these latter 2 grids during a second winter session each year from 2001-2004. Additional details about these study sites and trapping procedures can be found in Ladine (1995, 1997) and Vecchio (2011) for Meeman, and Baldwin (2003), Baldwin et al. (2006), Carver (2009), Carver et al. (2011), and Hisey (2012) for both Meeman and Ames. Sessions over all years on the 6 grids totaled to 112,000 trap nights. The

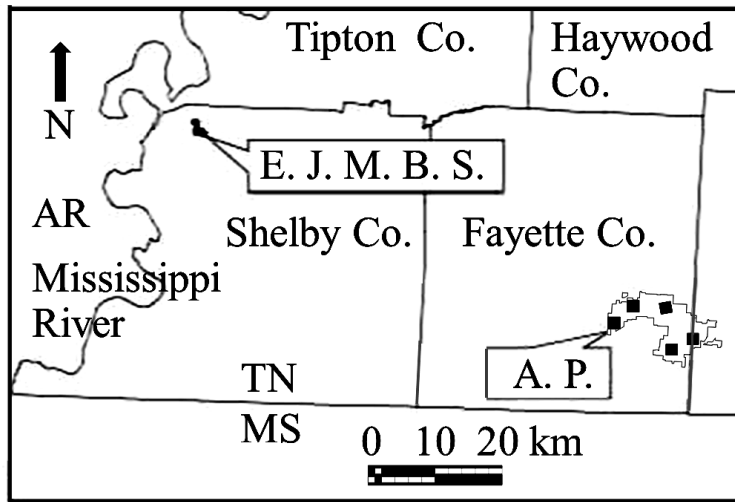


FIG. 1--Locations of the Edward J. Meeman Biological Station (E. J. M. B. S.) and the Ames Plantation (A. P.) in southwestern Tennessee, USA. AR, MS, and TN are Arkansas, Mississippi, and Tennessee, respectively. Symbols represent sites of trapping grids used in a study of temporal and spatial dispersion of closely related raccoons (*Procyon lotor*) across varied habitats and environmental conditions from 1991 to 2009. Grids at the Ames Plantation are, clockwise from left to right: Dusco Place, Pattersonville, Hancock Place, Afternoon Course, and Morning Course (from Carver 2009).

Institutional Animal Care and Use Committee of The University of Memphis approved these methods (IACUC Protocol #0016, investigator M. L. Kennedy). We immobilized animals as needed at first capture by intramuscular injection of 0.10 mg ketamine hydrochloride (Ketaset, Bristol Laboratories, Syracuse, NY 13201; Vetalar, Ketalar, Parke-Davis, Detroit, MI 48232) and 0.02 mg acepromazine maleate (The Butler Company, Columbus, OH 43228) per kilogram of body mass. We attached an M11 #3 tag (National Band and Tag Co., Newport, Kentucky) with an identification number to each of the 2 ears of each individual. For each capture, we recorded the Universal Transverse Mercator location codes, sex, weight, and lengths of the total body, tail, hind foot, and ear. Based on tooth wear, we assigned animals to the following age classes (Grau et al. 1970): age classes 1 (0-14 mo); 2 (15-38 mo); 3 (39-57 mo); 4 (58-86 mo); and 5 (>86 mo). During the trapping sessions from 2001-2006 and 2009 we preserved in 95% ethanol for genetic analysis tissue from ears of captured raccoons.

*Data analysis.*—We extracted DNA using the Puregene DNA Isolation Kit (Gentra Systems, Inc.) and quantified it using a VersaFluor fluorometer (Bio-Rad Laboratories). We used PCR primers for microsatellite loci G10B, G10C, G10X, Pfl4, Pfl9, Pfl11, Pl-35, Pl-40, and Pl-61 (Paetkau et al. 1995; Kays et al. 2000; Ary 2003; Hauver et al. 2010) to amplify target sequences, which we genotyped on an ABI 3730xl DNA Analyzer (Applied Biosystems, Foster City, CA, 94404). We included in the analyses samples for which at least half of the alleles were readable.

Initially, we completed standard population genetic analyses (Hisey 2012). Because of possible linkage disequilibrium, we excluded locus G10C from genetic analyses using the program *GenAlEx* 6.2 (Peakall and Smouse 2006). Using the program,



*COLONY* 2.0, we assigned or unassigned individuals to families of parents, full sibs, and half sibs via a maximum likelihood method using multilocus genotype data of multiple family members to increase statistical power (Wang 2004; Wang and Santure 2009). This analysis followed the full likelihood method under the assumption of both female and male polygamy without inbreeding. *COLONY* 2.0 allows for deviations from Hardy-Weinberg equilibrium, is moderately robust to nonrandom mating and linkage of markers, and accommodates genotyping errors and mutations (Wang and Santure 2009). We only excluded an individual as a candidate parent if its estimated birthdate was the same year as, or later than, that of the candidate offspring. We estimated the probability of including the true father and the true mother of an individual in the analysis at 0.106 and 0.088 respectively, and the genotyping error at 0.03. However, the use of error rate values varying over several orders of magnitude gives very similar results (Wang 2004). We accepted the run with the maximum likelihood out of 6 replicate runs of medium length and with medium likelihood precision. We determined the significance of differences among time periods or age classes for mean distances between locations of captures of full sibs by Kruskal-Wallis tests (Zar 1974; Conover 1999) using SAS 8.2 (SAS Institute, Inc., Cary, North Carolina). The terms dyad, trio, and quartet hereafter refer to groups of 2, 3, or 4 full sibs, respectively.

We analyzed spatial autocorrelation via the multiple Dclass option of the *GenAlEx* 6.2 (Peakall and Smouse 2006) program. This analysis generated the multilocus autocorrelation coefficient ( $r$ ), bounded by  $[-1, +1]$ , which indicated the genetic similarity between pairs of individuals with geographic separation falling within a specified distance class (Dclass). A correlogram plotted  $r$  and permutational and

bootstrapped 95% confidence intervals as a function of distance (Smouse and Peakall 1999; Peakall et al. 2003). The random permutation method assumed no spatial structure, calculated an autocorrelation coefficient ( $rp$ ) by the random shuffling of all individuals among the geographic locations. From 1000 such random permutations, the 25th and 975th ranked  $rp$  values indicated the upper and lower confidence limits around 0. The bootstrap method drew with replacement from within the set of pairwise comparisons for a specific Dclass. The program calculated the bootstrap autocorrelation coefficient ( $r_{bs}$ ) for each Dclass for each of 1,000 bootstrap trials. The 25th and 975th ranked  $r_{bs}$  indicated the 95% confidence limits around  $r$ . A calculated value of  $r$  located outside the permutational confidence interval around zero and a bootstrapping confidence interval around  $r$  that did not include  $r = 0$  inferred significant spatial genetic structure. This conservative approach favored acceptance of the null hypothesis for analyses with smaller sample sizes (Peakall et al. 2003). The analysis included individuals captured from fall 2000 through spring 2005 at both Meeman and Ames. It excluded captures of raccoons during the summer to eliminate the confounding effect of seasonal shifts in home ranges and of the limited numbers and spatial distribution of grids operated in the summer. We calculated values for  $r$  using distances between pairs of individuals captured only during the same year to reveal only dispersion of related individuals within years. We used the mean of all locations at which an individual was captured during a year as its position for that year.

RESULTS--*Sibship patterns*--We captured 390 raccoons 1087 times from 1991 to 2009 at Meeman and captured 449 raccoons 783 times from 2000 to 2005 at Ames, for a

total of 839 individuals captured 1870 times. Of the raccoons captured from 2001 to 2009 at the Ames and Meeman sites, we genotyped 440, an average of 78.0% of all raccoons captured each session. For the genotyped raccoons, the program, *COLONY* 2.0 (Wang 2004; Wang and Santure 2009) identified 111 individuals (25.2%), including 22.6% (65 of 288) of the males and 29.3% (44 of 150) of the females as members of 71 full sib dyads. Hereafter, we simply refer to these inferred sibs as sibs. Of these sibs, the sex for 2 and the age for 12 were unknown. Of the total of 70 dyads of full sibs with known geographic locations, individuals within a dyad were separated by a mean distance of 7.0 km (median value 636.4 m), by <1 km in 46 (64.7%) of the cases, by 2-13 km in 19 (27.1%) of the cases, and by >69 km in 5 (7.1%) of the cases (13.0% of full brothers). The mean distance between individuals within dyads of full sisters (350.1 m;  $SE = 115.3$  m;  $n = 14$ ) was only 3.14% of, and differed significantly from ( $T_1 = 12.4315$ ;  $P = 0.0004$ ), the mean distance between full brothers (11,153.0 m;  $SE = 5,207.6$  m;  $n = 24$ ). Mean locations of captures of full sisters were never as distant as 2 km apart but the locations of some full brothers were separated by over 80 km (Fig. 2). No significant differences among means existed ( $T_3 = 0.7999$ ;  $P = 0.8495$ ) for geographic distances between individuals of full sib dyads both captured at age class 1 (15,414.0 m;  $SE = 13,022.3$  m;  $n = 6$ ) vs. at age class 2 (8,805.4 m;  $SE = 7,575.1$  m;  $n = 9$ ) vs. at age class 3 (13,343.6 m;  $SE = 12,320.5$  m;  $n = 6$ ) vs. at combined age classes 4 and 5 (14,933.5 m;  $SE = 12,225.2$  m;  $n = 6$ ).

The months of November 2001-May 2003 were the end of a wet period with a monthly mean of 16.5 cm of precipitation. The months of June 2003-March 2005 were the beginning of a dry period with a monthly mean of 10.4 cm of precipitation. The

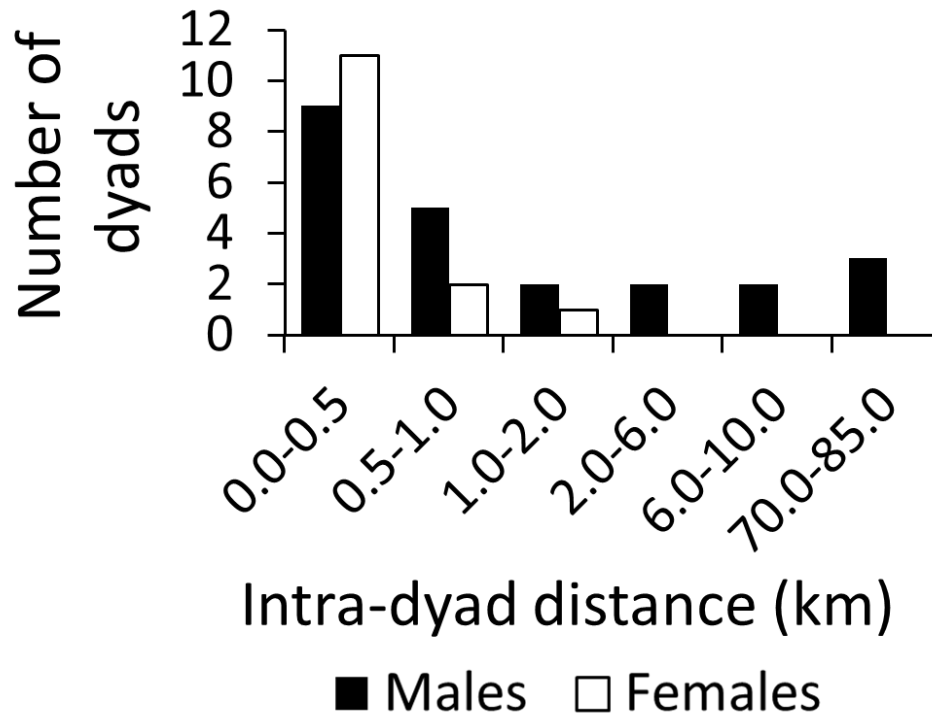


FIG. 2--Distance between mean locations of captures of individuals within dyads of full sisters or full brothers in the raccoon, *Procyon lotor*, determined as part of a study of the temporal and spatial dispersion of closely related raccoons across varied habitats and environmental conditions in southwestern Tennessee from 1991 to 2009.

mean distance between individuals within dyads of full sibs during the former (wet) timespan (3,846.9 m;  $SE = 2,419.1$  m;  $n = 33$ ) was 77.04% of the mean distance during the latter (dry) timespan (4,993.6 m;  $SE = 2,136.6$  m;  $n = 6$ ) but was not significantly different ( $T_1 = 1.4567$ ;  $P = 0.2275$ ). Considering individuals from Ames only, the mean from the former (wet) period (1,756.1 m;  $SE = 494.88$  m;  $n = 26$ ) was 23.68% of the mean from the latter (dry) period (7,146.78 m;  $SE = 2,597.7$  m;  $n = 4$ ) but was not significantly different ( $T_1 = 2.0560$ ;  $P = 0.1516$ ).

We captured the full sibs in only 22 of the total of 71 dyads of full sibs on the same grid in the same session, and in 34 of the 71 dyads, on the same grid in the same year but not necessarily within the same session. In only 3 of these dyads did we capture both of the individuals on the same grid together during more than one session, and in only 1 dyad did we capture them on the same grid together during a 3<sup>rd</sup> year. For the 18 dyads in which we captured the full sibs on different grids, we captured both sibs of only 1 dyad during the same session, sibs of 8 dyads during the same year, sibs of the other dyads a minimum of 1-8 years apart. In only 1 case did the captures of a dyad of sibs on the same grid during the same session or year during the wet period extend into the dry period (despite similar trapping effort during the former and the latter), and that was for the dyad that was found on the same grid together the longest—3 years.

Sibs within pairs were born 0-10 years apart, with a mean difference of 2.95 ( $SE = 0.30$ ;  $n = 60$ ) years, and 21.7% of these sibs born 5 or more years apart. The largest groups of full sibs that were identified in the current study were eight trios and one quartet of raccoons. Each of the individuals of three of the trios (one trio on Meeman and two trios on Hancock Place) were on the same grid during the same session. However,

for two of these trios (on Hancock, including three females, one male, and two of unreported sex), the individuals only remained on the same grid together for one session. The mean locations of capture of the individuals of each trio were separated by 701.6 and 849.3 m so that they were not highly cohesive temporally or spatially. The third of these three trios, on Meeman, comprised only females and all were first captured at age class 2 within 1 session of each other, with 2 of them first captured within 2 days of each other and last captured within 10 days of each other. This trio remained together on the same grid for over 1 year with 2 pairs remaining for over 1 year and 1 pair for over 3 years, making them the 3 pairs out of the entire 71 pairs of full sibs with the longest cohabitation on the same grid. The mean locations of capture of the individuals of this trio were separated by only 205.0 m. Of the other trios of full sibs, only two had as much as one pair of sibs each found on the same grid during a maximum time span of one session. None of the individuals of the one quartet of full sibs detected were on the same grid during the same session, though they all appeared there (Dusco Place) as differently-aged adults during the same year.

Dyads for which both sibs first appeared during the same trapping session as adults (age class 2 or older), on grids that had been trapped during prior sessions, comprised only 4 (5.6%) of all 71 dyads, with a mean and maximum geographic distance between sibs of a dyad of 359.1 and 949.8 m, respectively. Of these dyads, two were female-female, one was male-male, and one was female-unknown sex. An additional three dyads (4.2%) of full sibs that each appeared on the same grid during the same session included one sib that was at least age class 2 and one sib that was a juvenile (age class 1) with a birthdate at least 8 months prior and that might have already gone through

juvenile dispersal. The mean and maximum distances between the sibs within these three dyads were 475.5 m and 1,169.1 m, respectively. Of these three dyads, one was female-female and two were male-female. Together, these 7 dyads comprised 9.8% of all pairs of full sibs, with a mean separation of 409.0 m. Dyads of adult full sibs which both appeared first during the same year (including those captured during the same session) on the same grid that had been trapped during prior sessions, comprised 18 (25.3%) of the total of 71 full sib dyads. The mean and maximum distances between the sibs within these 18 dyads were 414.2 m and 1759.5 m, respectively. Of these 18 dyads, 8 were female-female, 3 were male-female, 6 were male-male, and 1 was female-unknown sex.

*Spatial genetic autocorrelation*--For grouped age classes, across years from November 2000 to March 2005, all values of  $r$  were positive, with the few exceptions noted as follows. The autocorrelation coefficient ( $r$ ) for grouped age classes had higher values among females than among males at all Dclasses analyzed and was significantly different between the sexes for some of the longer distances. For both sexes, values of  $r$  were positive and significantly different from 0 at all Dclasses and showed a general downward trend as the Dclass increased in size.

Raccoons of both sexes in age class 1 had values of  $r$  that were significantly different from 0 for Dclasses of 6,500 m or smaller (Figs. 3a, b). Females of age class 2-3 had values of  $r$  significantly greater than zero for all Dclasses (Fig. 3a). Compared to the values of  $r$  for the females of age class 1, the values for the females of age class 2-3 were similarly high for Dclasses of 6,500 m or smaller but higher above that Dclass. Females of age class 2-3 had much higher values of  $r$  than those of age class 4-5 at 260-520m but had lower values of  $r$  from 780 to 9,100 m. Age class 4-5 females had values

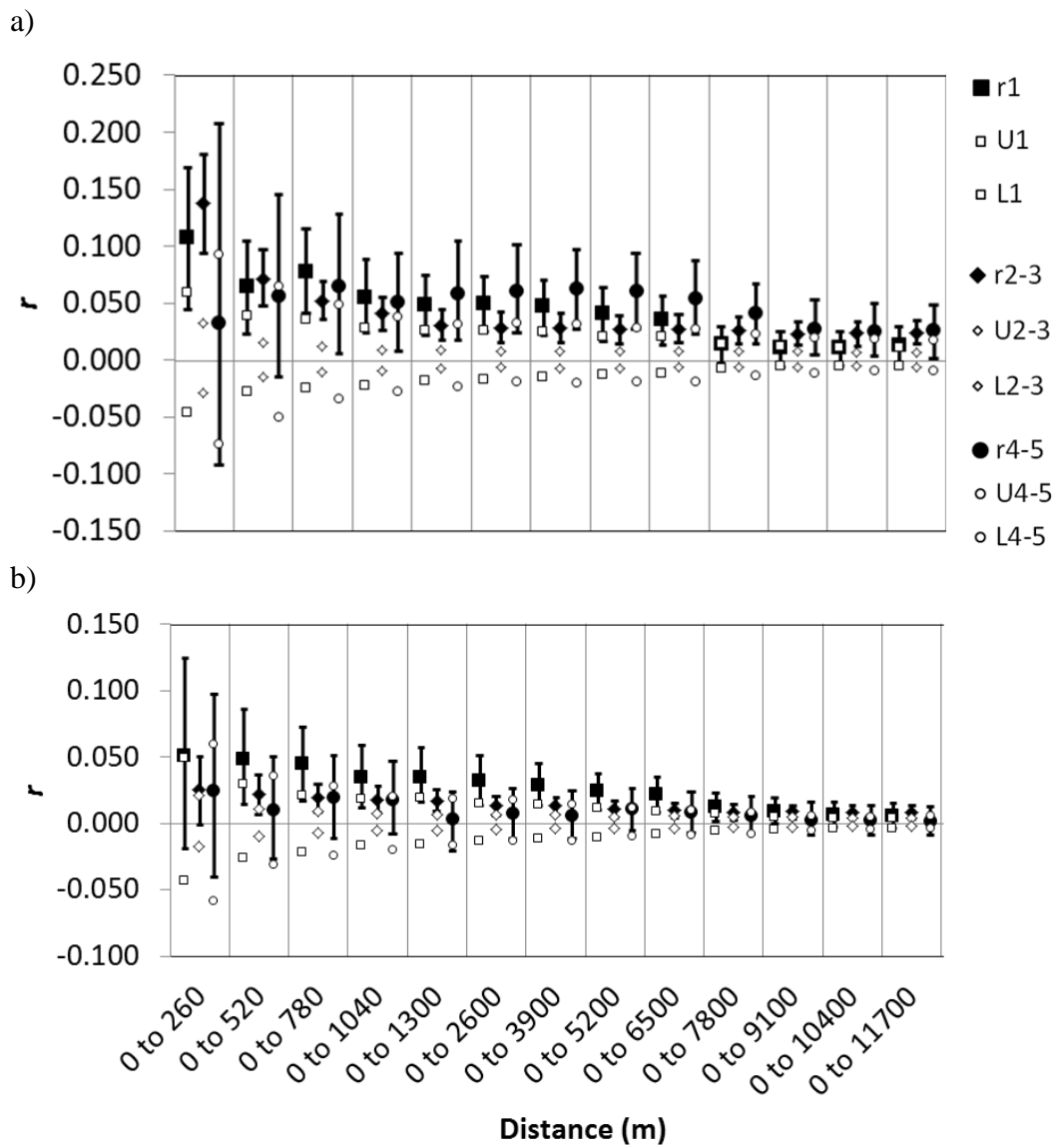


FIG. 3--Spatial genetic autocorrelation generated by the program, *GenAlEx* for microsatellite loci in the raccoon, *Procyon lotor*, continued on next page.



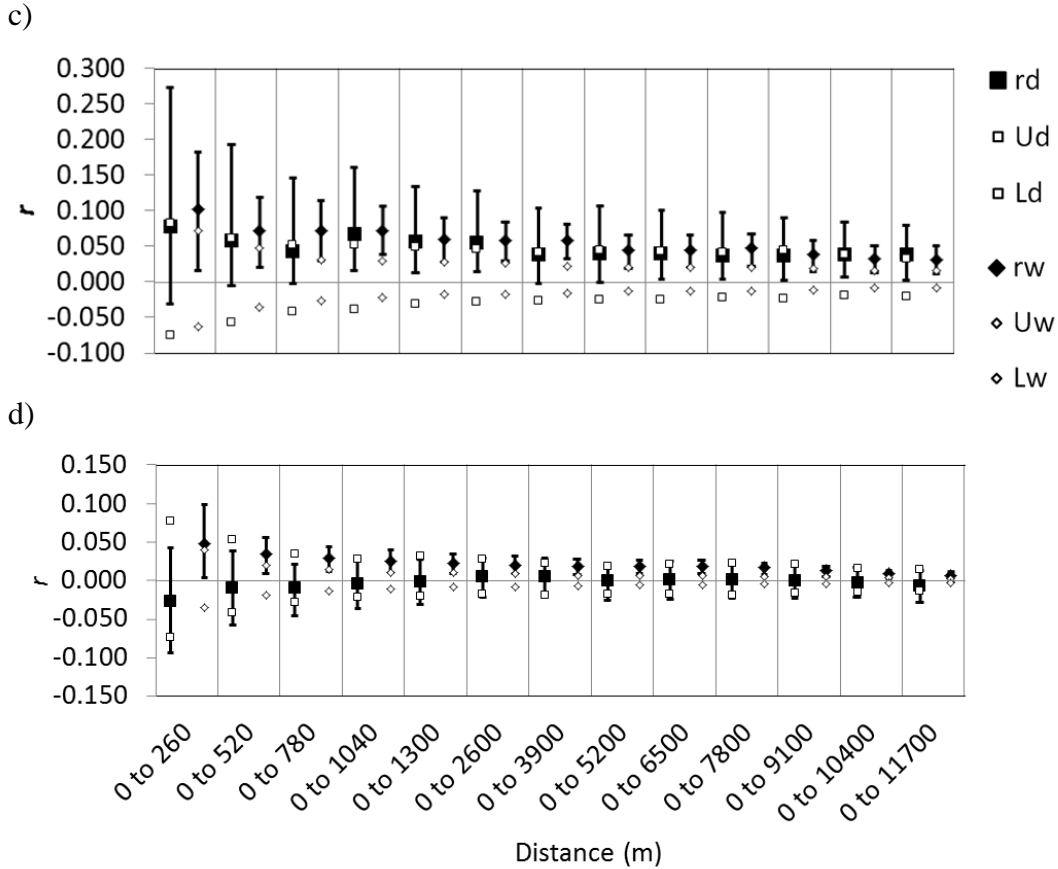


FIG. 3--Spatial genetic autocorrelation generated by the program, *GenAlEx* for microsatellite loci in the raccoon, *Procyon lotor*, continued from the previous page. Results were produced as part of a study of the temporal and spatial dispersion of closely related raccoons across varied habitats and environmental conditions in southwestern Tennessee from 1991 to 2009. Solid shapes designate the multilocus autocorrelation coefficient,  $r$ , indicating the genetic similarity between pairs of individuals with geographic separation falling within a specified distance classes of increasing sizes and at what distance positive autocorrelation declines. Vertical bars delimit the 95% bootstrapped confidence interval for  $r$ . Hollow shapes designate upper and lower limits (U and L, respectively) of the 95% permuted confidence interval around 0, assuming no spatial genetic correlation. If the calculated  $r$ -value falls outside the permutational confidence limits around 0 and the bootstrapping confidence interval around  $r$  does not include  $r = 0$ , then significant spatial genetic structure is inferred. Vertical overlap between the bootstrapped confidence intervals indicate that the values of  $r$  for the different groups of individuals within a given distance class are not significantly different. a) Females, and b) males. For a) and b),  $r_1$ ,  $r_{2-3}$ , and  $r_{4-5}$  are the autocorrelation coefficients among raccoons of age class 1, grouped age classes 2 and 3, and grouped age classes 4 and 5, respectively. c) Females, and d) males. For c) and d),  $r_d$  and  $r_w$  designate the autocorrelation coefficients among raccoons captured during the dry period and the wet period, respectively. See the text for further explanation of the analysis.

of  $r$  significantly greater than 0 at all Dclasses except 260-520 and 11,700 m. Among the males, those of age class 2-3 had small values of  $r$  more similar to those of age class 4-5 than to those of age class 1 (Fig. 3b). However, the values of  $r$  for males of age class 2-3 were significantly different from zero at all distances whereas those for age 4-5 were not significantly different than zero at any distance. Males consistently had lower values of  $r$  than females of the same age and Dclass.

For the combined sexes, the values of  $r$  across the different Dclasses during the wet period from November 2001 through May 2003 were from 1.4 to 5.1 times the values of  $r$  (mean = 2.5) during the dry period from November 2003 through March 2005. For the combined sexes, values of  $r$  were positive and significantly different than zero at all Dclasses during the wet period, but at all Dclasses during the dry period, the values of  $r$  were positive but not significantly different from zero. This effect was apparently due mostly to males for which a similar dichotomous pattern was evident, except that during the dry period they had values of  $r$  that were negative for some Dclasses and very near zero for all other Dclasses (Fig 3d). For females, the values of  $r$  for the wet period were greater than those values during the dry period for all Dclasses of 9,100 m or less, with the former being 1.78-0.84 (mean 1.21) times the latter across all Dclasses (Fig. 3c). For females, values of  $r$  during the wet period were positive and significantly different from zero across all Dclasses and during the dry period were positive at all Dclasses but not significantly different than zero at most Dclasses.

DISCUSSION--The present study incorporated regular collection of genetic data for 5-8 years and demographic data for 5-19 years from 839 raccoons on 13.8 km<sup>2</sup> of study

sites separated by up to 80 km. The scope of this study produced novel findings on the temporal and spatial dispersion of closely related raccoons across varied habitats and environmental conditions. The data did not support the prediction that closely related raccoons would remain geographically clustered over multiple years (Ratnayeke 1997; Gehrt and Fritzell 1998a, b; Ratnayeke et al. 2002). Though we captured most sibs within 1 km of each other, we rarely captured them during the same year or over extended time spans. In addition, the higher distances between sibs and the loss of general genetic relatedness of raccoons over short distances during drier years supported the prediction of an association between spatial dispersion and environmental conditions (Gehrt 2003).

*Sibship patterns*--In the current study, the remarkably high mean separation of full sib pairs (7.0 km) was largely the effect of the notable percentage (7.1%, including 13.0% of full brothers) separated by distances of over 68 km. Although some mean distances between sibs differed markedly by age group or precipitation level, the differences were not significant. The trends among age classes suggested wide dispersion in juveniles, possibly followed in young adulthood by some loss of the most distant dispersers or a return toward the natal home range. The trends also suggested gradual home range shifts as adults age, which result in greater distances from the natal site. A few juvenile female raccoons in eastern Tennessee dispersed and then returned toward the natal home range (Ratnayeke 1997). Each age class in the current study had substantial long-distance dispersion with mean separation between sibs of the same age class varying from about 8.8 to 15.4 km, and 11.1-16.7% of pairs separated by more than 69 km. Use of an assignment test on the data from the current study indicated that 19 of

441 raccoons from the Ames or Meeman sites possessed genotypes consistent with having 1 parent from the genetic cluster typical of the opposite site (Hisey 2012). Other studies of raccoons observed high levels of dispersal by juvenile males (Gehrt and Fritzell 1998a), with rare instances over extreme distances (Priewert 1961; Lynch 1967; Tabatabai 1988), and lower genetic relatedness among local males than among local females (Ratnayeke 1997; Ratnayeke et al. 2002; Cullingham et al. 2008a). Little has previously been reported for raccoons on the distance of dispersion of separate age classes of adults.

Of interest in the current study was the trend in distances between sibs during multi-year changes in precipitation that might alter quality of habitat and the tendency to form lineages. Raccoons in western Tennessee preferentially use habitats in forests and near water sources (Allsbrooks and Kennedy 1987; Baldwin 2003; Baldwin et al. 2006), consistent with findings of other studies (Fritzell 1978; Kaufmann 1982). Prior studies on raccoons found highly related females exhibiting site fidelity to their natal home ranges, and thus, remaining in close proximity for multiple years, suggestive of lineage formation for this solitary carnivore (Ratnayeke 1997; Gehrt and Fritzell 1998a, b; Ratnayeke et al. 2002). However, these studies were in favored habitats over restricted periods of time of 3 years or less, and climate data (NCDC, Asheville, North Carolina) reveals that they were during favorable periods of higher than average precipitation. Ladine (1995), in a study of raccoons at Meeman, and Gehrt (2003), in a review of this species across its range, speculated that fidelity to sites might be associated with availability of resources, with higher rates of long-term fidelity to sites occurring in

favorable habitats and when resources are predictable between years, but dispersal occurring when resource availability changes.

Based on these factors, the expectations might be for the buildup of lineages to be highest and the distances between sibs to be lowest at the end of wet periods, and these effects to reverse at the beginning of dry periods. In the current study, the mean distance between full sibs captured during the wet period from November 2001 to May 2003 (NCDC, Asheville, North Carolina) was considerably less than, but did not differ significantly from, the mean distance between full sibs captured during the dry period from June 2003 to March 2005. The low level of significance of this difference was influenced by the inclusion of 1) all of the full sibs from Meeman with only small distances between them limited by the size of the grid, and 2) the few dyads that were separated by the very large distances between Ames and Meeman. When we excluded the data from Meeman and only considered the data from Ames, the mean distance between full sibs captured during the wet period was less than  $\frac{1}{4}$  of the mean distance between full sibs captured during the dry period. Though this is a striking trend, the difference was still not significant, possibly because the number of pairs of sibs captured at Ames during the dry period was very low ( $n = 4$ ), and the wet period was not long enough for the accrual of extended lineages. Such lineage formation can require multiple generations remaining in stable groups (Chesser 1991b; Gehrt and Fritzell 1998a).

Little has been previously reported on direct study of sibships in raccoons, or on distances of shifts in home ranges of raccoons during consecutive years. Data on such shifts are likely to be biased because of the difficulty of locating individuals both before and after long-distance dispersal (Gehrt and Fritzell 1998a; Gehrt 2003). For the small

proportion of raccoons recaptured in consecutive years in other studies, most were found to have moved <5km (Rosatte et al. 2007, 2010); and for parous females, 21% to have moved <1 km and 5.9% to have moved 1-3 km (Cullingham et al. 2008a). Other studies on raccoons also have suggested limited female dispersal (Gehrt and Fritzell 1998a; Ratnayeke et al. 2002; Cullingham et al. 2008b).

Despite the very high distance between a few full sibs and the variability in this distance associated with sex, age, and precipitation in the current study, the distance between most full sibs was low (<1 km in 64.7% of the dyads; median value 636.36 m), and especially between full sisters (mean of 350.1 m). From these distances, one might suppose that lineage formation would be common in raccoons and would be biased toward female membership (Ratnayeke 1997; Gehrt and Fritzell 1998a, b; Ratnayeke et al. 2002). The mating system for raccoons has been described as polygamous or promiscuous (Gehrt and Fritzell 1999; Roy Nielsen and Nielsen 2007). However, in the current study, full sib dyads, trios and quartets comprised more than 25% of genotyped individuals, and these sibs were born up to 10 years apart. These findings suggest that a considerable proportion of parental pairs are in the area over long time spans and reproduce repeatedly, which could contribute to the development of lineages. Nonetheless, other findings of the current study and prior reports of high turn-over in this species (Johnson 1970; Moore and Kennedy 1985; Stevens et al. 1995; Maris 1998) challenge the view that lineages might be common in raccoons. In the current study, for full sibs captured on the same grid, the proportions captured during 1) the same year though not necessarily the same session; 2) the same session; 3) each of the same multiple sessions; and 4) each of the same 3 years, were 47.9, 31.0, 4.2, and 1.4% of all

full sib pairs, respectively. Therefore, the proportion of sibs captured together over longer periods of time was small in the current study, unlike the multi-year clusters of close relatives found during restricted periods of favorable environmental conditions and in preferred habitats in other studies of raccoons (Ratnayeke 1997; Gehrt and Fritzell 1998a, b; Ratnayeke et al. 2002). Offsetting the overall rarity of lineages in the present study, the presence of eight trios and a quartet of full sibs on the study sites is suggestive of the development of a few substantial lineages. However, sib pairs comprising these few larger groups also only rarely remained on the same grid together at the same time period. Additionally, despite similar trapping effort during each of these periods, in only 1 case did the capture of a dyad of sibs on the same grid during the same session or year during the wet period extend into the beginning of the dry period, and that was for the dyad that was found on the same grid together the longest (3 years).

In the current study, we detected groups of closely related raccoons rarely, generally only over very short durations and seldom continuing past the end of the wet period and into the dry period. These patterns do not suggest the common development of lineages of closely related individuals living over long periods of time in stable home ranges that overlapped or were adjacent. Another possible pattern of lineage development is fidelity to groups of closely related individuals that shift home ranges together, such as is exhibited by some mammals (Rood 1989; Waser et al. 1994; Nelson and Mech 1999). In the current study, such a pattern would be detected as full sibs that were first captured in close spatial and temporal proximity. The full sib pairs that were first captured on the same grid during the same session or same year only comprised about 10% and 25% of all sib pairs, respectively. Though these pairs were composed of

more females than males, the males contributed a substantial component. It appears from these data that close relatives did not commonly disperse together and that in cases in which they possibly did, they consisted of either sex unlike other mammalian species (Rood 1989; Waser et al. 1994; Nelson and Mech 1999).

*Spatial genetic autocorrelation*--Though the trapping methods used have been found to reliably recapture raccoons remaining on sites (Gehrt and Fritzell 1996), the loss of full sibs from the grids and limited sample sizes in the current study constrained the comparisons of patterns of movements of first order relatives of different ages, sexes, or during different precipitation levels. These limitations were reduced by spatial analysis of genetic autocorrelation among all genotyped individuals as described in Peakall and Smouse (2006). For many of the groups of raccoons partitioned by sex, age class, or levels of precipitation in the current study, the value of the genetic autocorrelation coefficient,  $r$ , was highest at the smallest Dclasses. Such a pattern indicates the positive genetic correlation generated by the portion of related individuals that have undergone minimal dispersal from the natal home range (Double et al. 2005). Values of  $r$  declining with increasing sizes of Dclasses indicates fewer related individuals dispersing to increasing distances (Peakall et al. 2003). By definition, the value of  $r$  must reach 0 at a distance that includes all individuals in the analysis, which was about 80,000 m in the current study.

The values of  $r$  for age class 1 raccoons of both sexes generally declined most steeply from the smallest through the 780 m Dclass and remained positive and significantly different from 0 through the 6,800 m Dclass in the current study. Such a pattern would indicate (Peakall et al. 2003; Double et al. 2005) that most related juvenile



raccoons remained within a few hundred meters of their natal sites but that some significant positive correlation existed due to related individuals dispersing as far as 6,800 m. No departure from a random distribution of genotypes is indicated by  $r$  values not significantly different from 0 (Double et al., 2005) such as were found in the current study for Dclasses above 6,800 m. Near the northern limits of the range of the raccoon (Gehrt 2003) in Ontario, Canada most related juveniles of either sex appeared to have remained within about 3,000 m of each other but a significant portion appeared to have dispersed at least 7,500 m (Cullingham et al. 2008a).

The values of  $r$  for female raccoons of combined age classes 2 and 3 were similar to those of the juvenile females. However, the former values differed by being higher than those of the younger females and significantly different from 0 at Dclasses above 6,800 m. Such a pattern in values of  $r$  (Double et al. 2005) would indicate significant positive genetic structure due to dispersal of related raccoons at least as far as the 11,700 m maximum for this analysis. Females of the combined age classes 4 and 5 had values of  $r$  very similar to those of females of the combined age classes 2 and 3 except that in the 260 and 520 m Dclasses they were much lower and not significantly different from 0 and in the 780-9,100 m Dclasses were higher. Such a pattern in values of  $r$  (Peakall et al. 2003; Double et al. 2005) would indicate no significant positive genetic structure in the 260-520 m Dclasses because the remaining females of age classes 4 and 5 had dispersed further away from their natal home ranges. For female raccoons in Ontario, the values of  $r$  for adults also were lower than those for juveniles but differed significantly from zero at all Dclasses (Cullingham et al. 2008a).

Among the males in the current study, those of combined age classes 2 and 3 had small values of  $r$  more similar to those values of combined age classes 4 and 5 than to those values for age class 1 but significantly different from zero at all distances. Such a pattern in values of  $r$  (Double et al. 2005) would indicate that compared to age class 1, a much higher portion of individuals of age classes 2-3 had dispersed away from natal home ranges, and that a substantial number of related raccoons were dispersed at least as far as 11,700 m. The values of  $r$  for age class 4-5 males did not differ significantly from zero at any distance. Such a pattern in values of  $r$  (Peakall et al. 2003; Double et al. 2005) would indicate that these individuals were so completely dispersed that there was no significant spatial genetic structure or departure from a random distribution of genotypes. For male raccoons in Ontario, the values of  $r$  for juveniles were greater than 0 and differed significantly from 0 for all Dclasses up to the maximum analyzed distance of 7,500 m, but for adults did not significantly differ from 0 for any except the 750 m Dclass (Cullingham et al. 2008a). One might expect that older females would accrue clusters of close relatives (Ratnayeke 1997; Gehrt and Fritzell 1998a, b; Ratnayeke et al. 2002). However, trends in the current study for both sibships and genetic autocorrelation are toward older adults of each sex having undergone more complete dispersion to greater distances than younger adults.

The autocorrelation analysis supported the prediction that the spatial dispersion of kin would be affected over multiple years by varying environmental conditions. A significant positive genetic structure indicates the clustering of relatives (Double et al. 2005), as opposed to no significant departure from a random distribution of genotypes because of the dispersal of relatives (Peakall et al. 2003; Double et al. 2005). At all

Dclasses for the combined sexes and age groups, we found the former during the wet period and the latter during the dry period. We found similar patterns in females in the current study. During the dry period, this pattern contrasted with findings for raccoons in Ontario, for which the value of  $r$  differed significantly from zero for both juvenile and adult females at all examined Dclasses (Cullingham et al. 2008a). Lineages can form due to limited female dispersal from natal home ranges (Chesser 1991a; Ratnayeke 1997; Gehrt and Fritzell 1998a; Ratnayeke et al. 2002). However, in the current study, values of  $r$  and their significance suggested that any such tendency during wet periods might be followed by some abandonment of such lineages due to longer-range dispersal during dry periods. This effect was more prominent in males. Clustering of relatives resulting in values of  $r$  greater than, and significantly different from zero (Double et al., 2005) was found in males during the wet period of the current study for all Dclasses examined. In contrast, during the dry period, values of  $r$  were negative up to about 1,000 m, although not significantly different from 0, consistent with such complete movement away from natal sites that relatives were more dispersed than a random distribution. Values of  $r$  very near zero are consistent with such heavy long-distance dispersal that little or no genetic clustering occurs (Peakall et al. 2003; Double et al. 2005). We found such a pattern at all higher Dclasses through 11,700 m for males during dry periods. These patterns of greater dispersion of related individuals during the dry period were consistent with the trend toward greater distances between siblings during the dry period than during the wet period in the current study. Over 14 years at Meeman, raccoons disappeared at the highest rates during dry periods and established a much greater number of long-term residencies during wet periods (Hisey 2012).

The values of  $r$  derived in the current study in the southern USA were generally much lower than those values for the same age or sex of raccoons in Ontario (Cullingham et al. 2008a), near the northern limits of the range of this species (Gehrt 2003). Across most of the range of the raccoon in the southern USA, wet periods spanning 1-2 years, and associated with the climatic pattern of the El Nino Southern Oscillation, occur every 3-7 years (Raven et al. 2010). High levels of dispersion among related individuals found during the dry period in the current study and residual effects during the wet period might reduce the values of  $r$  relative to those values in geographic areas that experience less of these cyclic climatic effects. The tendency for each sex to remain as residents or disperse also varies geographically in some other species of mammals and birds (Foster and Endler 1999).

Though clustering of other close relatives can contribute to the development of lineages, the patterns for full sibs should serve as useful indicators of the prevalence and spatio-temporal dispersion of closely related raccoons. Comparisons of dispersion patterns of groups of full sibs separated by sex, age, or level of precipitation assume that for each of these groups the mean distances between the birthplaces of sibs due to movements of the pairs of parents are similar. Such movements of parents might affect the overall dispersion of the sibs and the prevalence of clusters of close relatives. In the current study, the spatial patterns in genetic autocorrelation were in general agreement with patterns in dispersion of close relatives as indicated by full sibs and did not reveal the prevalent clusters of closely related individuals that were found in some other studies (Ratnayeke 1997; Gehrt and Fritzell 1998a, b; Ratnayeke et al. 2002).

Movement patterns in some solitary carnivores like raccoons are of special interest because of their 1) rapidly increasing populations (Sanderson 1987), 2) impacts on agriculture (Gehrt 2003) and prey species of conservation concern (Garrott et al. 1993; Jennings et al. 2006), and 3) spreading of disease (Gehrt 2003). Raccoon rabies is the greatest epizootic on record, is rampant along the Atlantic seaboard, and has recently extended westward (Gehrt 2003). It might threaten the states to the west of the Appalachians where the current study was located but where this form of rabies has not been observed (Gehrt 2003; Cullingham et al. 2008b). The current study identified substantial long-distance dispersion, especially by males and during dry conditions. These patterns might be found over the major portions of the range of the raccoon characterized by periodic environmental change which can stimulate dispersal. Future management strategies should recognize the importance of these patterns in the spreading of disease (Coyne et al. 1989; Macdonald and Laurenson 2006) and recolonizing areas in which pest individuals have been removed (Gehrt 2003).

This study produced novel findings by monitoring spatio-temporal dispersion of relatives with similar intensity across habitats and multi-year changes in environmental conditions that varied in preference by raccoons (Kaufmann 1982; Allsbrooks and Kennedy 1987; Gehrt and Fritzell 1998b; Baldwin et al. 2006). Novel aspects included determination that sib groups of substantial size or duration at a location, or shifting locations together, rarely occurred. The spatial patterns of related raccoons found in the present study accentuated the importance of dispersion during dry periods and by individuals of older age classes, and of long-distance movements, especially in males. We detected these patterns only through genetic analysis. Little has been previously

reported on these aspects of the movements and clustering of relatives in solitary mammals. Other studies that did not incorporate genetic patterns have detected long-distance dispersal in raccoons but at extremely low rates (Priewert 1961; Lynch 1967; Tabatabai 1988; Rosatte et al. 2010). Studies of limited duration during wet periods and in favored habitats have concluded that lineage formation promoted by female philopatry might lead to cooperative behaviors and the evolution of gregariousness in raccoons (Ratnayeke 1997; Gehrt and Fritzell 1998; Ratnayeke et al. 2002). Considering the patterns distinguished in the current study, further evaluation of the prevalence of lineages and long-distance movements in raccoons might be needed in parts of their range characterized by less favored habitats or patterns of environmental instability such as multiannual fluctuations in precipitation.

CONCLUSION--1. The extensive scope of this study produced novel findings on the temporal and spatial dispersion of closely related raccoons across habitats and multi-year changes in environmental conditions that varied in preference by raccoons but were monitored with similar intensity. This study incorporated collection of genetic data for 5-8 years and demographic data for 5-19 years from 839 raccoons captured 1870 times on 13.8 km<sup>2</sup> of study area spanning some 80 km.

2. Distances between full sibs were generally low (<1 km in 64.7% of the dyads; median value 636.36 m) and especially between full sisters (mean of 350.1 m).
3. The proportion of sibs captured on the same grid in the same trapping sessions over a year or more was small. These patterns would not facilitate the development of gregariousness.

4. During drier years, distances increased between sibs and significant genetic relatedness of raccoons over short distances was lost.
5. Sib groups shifting locations together, or of substantial sizes or durations at fixed locations, were rare events.
6. The greatest dispersion was between males and between individuals of older age classes. The oldest age classes of each sex exhibited no significant clustering of relatives at least over shorter distances. Each age class had substantial long-distance dispersion with mean separation between sibs of the same age class varying from about 8.8 km to 15.4 km and 11.1 - 16.7% of sibs being separated by more than 69 km.
7. High levels of dispersion, such as were observed especially in males or during the dry period, could speed the spread of key diseases like raccoon rabies.
8. Patterns distinguished in the current study suggest the need for further investigation of the prevalence of kin clusters and long-distance movements in raccoons in broad regions of their range characterized by less favored habitats or environmental changes such as multiannual fluctuations in precipitation. Future management strategies should recognize the importance of these patterns in the spreading of disease and recolonizing areas in which pest raccoons have been removed.

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## **Chapter V. Conclusion**

The current study was the most geographically extensive and longest-term uninterrupted investigation to date of the dispersal, residency, and spatial-genetic patterns of raccoons. The broad scope of this study produced novel findings on the temporal and spatial dispersion of individuals across habitats and multi-year changes in environmental conditions that varied in preference by raccoons.

Greater dispersion of raccoons occurred during multi-year periods of low than during high precipitation, as indicated by much less common establishment of long-term residencies, greater distances between full sibs, and loss of significant relatedness among raccoons over short distances. High annual rates of disappearance from sites (turn-over) were displayed by both sexes, but these rates were 100% for the youngest and oldest males. A few raccoons were recaptured over 3-11 winters to become long-term residents, but this was rare even among females and particularly for those on natal home ranges. Seldom did groups of full sibs shift locations together, comprise more than three individuals, or remain intact in the same vicinity for more than a year though the median distance between full sibs was low. The spatial dispersion among closely related raccoons was greater in males than in females and in older adults than in younger adults. Genetic differentiation in microsatellite alleles between local, area, and transcontinental sites appeared to be increased by: 1) geographic distance (isolation by distance, or IBD) at all 3 scales; 2) females remaining on local sites; and 3) landscape barriers to movement. However, a substantial portion of individuals sampled showed evidence of movement between sites 75-1200 km apart.

The temporal and spatial instability observed in raccoons on the study sites, including sib groups, would not facilitate lineage-structuring in populations or their genetics or the development of gregariousness within lineages. The frequent dispersal at the end of dry periods, after severe winter weather, and during all years for juvenile males, and the substantial long-distance dispersal that were apparent in the current study could hasten the spread of key diseases like raccoon rabies. The mountains and deserts of western North America might help block the spread of raccoon-borne diseases, especially if control measures are applied in the Southwest where a low level of migration has apparently occurred. However, the Appalachians are unlikely to help block such diseases. Other extended studies are necessary to determine the prevalence of these demographic and genetic patterns in additional parts of the raccoons range such as those characterized by less favored habitats or periodic multiannual changes in the environment. Future management strategies should recognize the importance of these patterns in the spread of disease and the recolonization of areas in which pest raccoons have been removed. All results reported in this study were based primarily on my work with the exceptions of extensive assistance in the field by students and staff members of The University of Memphis and in genotyping by Génome Québec.

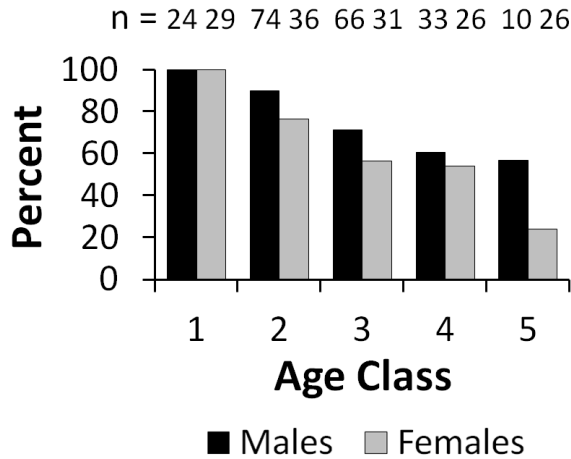
## APPENDIX I

Rates of turn-over and first appearance among age and sex classifications for raccoons (*Procyon lotor*) captured during winters from 1991 to 2004 at the Meeman Biological Station in western Tennessee.

Animals captured were assigned to the following age classes (Grau et al. 1970): age classes 1 (0-14 mo); 2 (15-38 mo); 3 (39-57 mo); 4 (58-86 mo); and 5 (>86 mo).

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GRAU, G. A., G. C. SANDERSON, AND J. P. ROGERS. 1970. Age determination of raccoons. *The Journal of Wildlife Management* 34:364-372.



**FIG. 1.**—Rates of 1<sup>st</sup> appearance of raccoons (*Procyon lotor*) by sex and age class at the Meeman Biological Station in western Tennessee. Of (n) individuals in each sex and age class captured during any winter 1991-2004, the proportion not captured the previous winter is the percent of first appearance. The same individual could be present during more than 1 year in the same or different age class and was counted and used in the calculations again each additional year it was present. See text for explanation of age-class categories.

**TABLE 1.**—Turn-over rates (the percentage of all individuals captured on a site during a year that were not recaptured there the following year) of raccoons (*Procyon lotor*) by sex and age class at the Meeman Biological Station in western Tennessee. Values in table are: total numbers of individual raccoons in each sex and age class captured during any winter 1991-2003; numbers captured during a year that were recaptured the following year, numbers captured during a year that were not recaptured the following year, percent of individuals captured during a year that were recaptured the following year, and percent of individuals captured during a year that were not recaptured the following year (=annual turn-over rate). Each individual was considered as a separate independent trial. See text for explanation of age-class categories.

Trend	Age class				
	1	2	3	4	5
Males captured, total	22	70	45	22	7
Males recaptured the following year	0	17	9	2	0
Males not recaptured the following year	22	53	36	20	7
% males recaptured the following year	0.0	24.3	20.0	9.1	0.0
Male turn-over rate (%)	100.0	75.7	80.0	90.9	100.0
Females captured, total	27	35	18	15	7
Females recaptured the following year	5	12	4	5	2
Females not recaptured the following year	22	23	14	10	5
% females recaptured the following year	18.5	34.3	22.2	33.3	28.6
Female turn-over rate (%)	81.5	65.7	77.8	66.7	71.4

## APPENDIX II

Detailed methods in capturing and processing raccoons (*Procyon lotor*) at trapping grids in southwestern Tennessee as part of a study to determine genetic structure of microsatellite loci at multiple scales across the United States and Canada.

*Trapping procedures.*—At the Ames Plantation in Fayette and Hardeman counties (hereafter termed, “Ames”), southwestern Tennessee, 5 grids separated by a mean distance of 5.2 km (minimum 1.6 km) were established (Fig. 1). Each comprised an 8 by 8 array of 64 raccoon-sized Havahart (Woodstream Corporation, Lititz, Pennsylvania) or Tomahawk (Tomahawk Live Trap Co., Tomahawk, Wisconsin) live traps spaced at approximately 230 m and covering 259 ha. Approximately 75 km northwest at The University of Memphis' Meeman Biological Station (hereafter termed, “Meeman”), near Millington, Shelby Co., Tennessee, a 6th grid was established, comprising a 5 by 10 array of 50 traps spaced at approximately 150 m and covering 81 ha (Ladine 1995, 1997). Habitat at the grids included upland and bottomland forests, crops, oldfields, kudzu, ponds and intermittent streams, and adjacent to 3 of the grids at Ames, the North Fork of the Wolf River (Baldwin 2003; Carver 2009).

Mark-recapture trapping sessions comprised about 2000 trap nights (1 trap night = 1 trap set for 1 night). Sessions were conducted at the grid at Meeman during 40 selected days spanning the winter breeding season each year for 1991-2006 and 2008-2009 and spanning the summer rearing seasons of 2001-2003. At Ames, sessions each comprised 32 selected days. They were conducted spanning the winter breeding season from fall 2000 to Spring 2005 and the summer rearing season from 2001-2003. Sessions were conducted at each of the 5 grids during each winter, at 2 of the grids during each summer, and at 1 of the latter during a second winter session each year from 2001-2004. Additional details about these study sites and trapping procedures may be found in Baldwin (2003), Baldwin et al. (2006), Carver (2009), Carver et al. (2011), Ladine (1995, 1997), and Vecchio (2011). Trapping sessions over all years at the 6 grids totaled



to 112,000 trap nights. Methods followed the guidelines for the use of wild mammals in research suggested by the American Society of Mammalogists (Sikes et al. 2011) and were approved by the Institutional Animal Care and Use Committee of The University of Memphis (IACUC Protocol #0016, investigator M. L. Kennedy). When animals were first captured, they were immobilized as needed by intramuscular injection of 0.10 mg ketamine hydrochloride (Ketaset, Bristol Laboratories, Syracuse, New York 13201; Vetalar, Ketalar, Parke-Davis, Detroit, Michigan 48232) and 0.02 mg acepromazine maleate (The Butler Company, Columbus, Ohio 43228) per kg body mass. An M11 #3 tag (National Band and Tag Co., Newport, Kentucky) with an identification number was attached to each of their ears. For each capture, the Universal Transverse Mercator location codes, sex, reproductive condition, mass, estimate of age class from tooth wear (Grau et al. 1970), and lengths of the total body, tail, hind foot, and ear were recorded. Samples of tissue were taken from ears of captured raccoons during the trapping sessions from 2001-2006 and 2009 and preserved in 95% ethanol for genetic analysis.

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### APPENDIX III

Detailed results of analyses of genetic structure at 8 microsatellite loci of the raccoon (*Procyon lotor*) at 3 geographic scales across the United States and Canada: transcontinental, southeastern area, and local southwestern Tennessee sites.

Tables 1 and 2 provide mean and standard error (SE) for observed and expected heterozygosity ( $H_o$  and  $H_e$ , respectively) for 8 microsatellite loci for raccoons (*Procyon lotor*) sampled at 3 geographic scales across the United States and Canada. For all loci combined,  $H_o < H_e$  for each of the 6 transcontinental regions, 10 of 14 transcontinental states, 4 of 9 sites in the southeastern area, and each trapping grid sampled in southwestern Tennessee (Table 1). Over the combined populations,  $H_o < H_e$  for transcontinental regions at 6 of 8 loci, for transcontinental states at 6 of 8 loci, for sites in the southeastern area at 4 of 8 loci, and for trapping grids in southwestern Tennessee at 7 of 8 loci (Table 2).

Tables 3 and 4 provide the results of global tests for the alternate hypothesis of heterozygote deficit. The tests in Table 3 are for each separate population across the combined 8 loci analyzed, and the tests in Table 4 are for each separate locus across the combined populations at a given geographic scale.

Table 5 provides the number of migrants per generation and Nei (1987) standard genetic distance between paired sites at each geographic scale.

Figure 1 provides plots and Mantel test correlations between geographic distance and log Nei genetic distance between pairs of populations.

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**TABLE 1.**—Continued on following pages. Mean and standard error (SE) of observed and expected heterozygosity ( $H_o$  and  $H_e$ , respectively) for each population over the 8 microsatellite loci analyzed for n individual raccoons (*Procyon lotor*) that were sampled to determine genetic structuring at 3 scales across the United States and Canada. Scales included: a) transcontinental regions; the site of the population (Pop.) for NW (Northwest) included Oregon only; NMW (Northern Midwest) included Manitoba and Wisconsin; NE (Northeast) included New York and Vermont; EC (East Central) included Indiana, Kentucky, and Tennessee; SMW (Southern Midwest) included Texas, Louisiana, Arkansas, and Kansas; and SE (Southeast) included Alabama, Georgia, and South Carolina. b) Transcontinental states; the sites of the populations were identified by state and province abbreviations for Alabama, Arkansas, Georgia, Indiana, Kansas, Kentucky, Louisiana, Manitoba, New York-Vermont, Oregon, South Carolina, Tennessee, Texas, and Wisconsin, respectively. c) Southeastern area; the sites of the populations were, respectively, Arkansas, Georgia, Indiana, eastern Kentucky, western Kentucky, South Carolina, northeastern Tennessee, northwestern Tennessee, and southwestern Tennessee. d) Trapping grids in southwestern Tennessee. Identifiers were M for the Edward J. Meeman Biological Station; and for the Ames Plantation, AC, D, H, MC, and P were grids at Afternoon Course, Dusco Place, Hancock Place, Morning Course, and Pattersonville, respectively.

a)

Pop.	n		$H_o$	$H_e$
EC	540	Mean	0.524	0.580
		SE	0.096	0.108
NE	13	Mean	0.533	0.539
		SE	0.100	0.103
NMW	30	Mean	0.536	0.563
		SE	0.098	0.111
NW	15	Mean	0.425	0.448
		SE	0.116	0.097
SE	17	Mean	0.473	0.551
		SE	0.123	0.111
SMW	41	Mean	0.572	0.650
		SE	0.111	0.077

**TABLE 1.**—Continued. Mean and standard error (SE) of observed and expected heterozygosity ( $H_o$  and  $H_e$ , respectively) for each population over the 8 microsatellite loci analyzed for n individual raccoons (*Procyon lotor*) that were sampled to determine genetic structuring at 3 scales across the United States and Canada.

b)

Pop.	n		$H_o$	$H_e$
AL	6	Mean	0.483	0.466
		SE	0.122	0.116
AR	11	Mean	0.632	0.616
		SE	0.115	0.073
GA	5	Mean	0.369	0.528
		SE	0.125	0.082
IN	6	Mean	0.458	0.490
		SE	0.098	0.106
KS	12	Mean	0.580	0.590
		SE	0.109	0.084
KY	34	Mean	0.483	0.534
		SE	0.125	0.122
LA	5	Mean	0.550	0.628
		SE	0.150	0.081
MB	15	Mean	0.473	0.509
		SE	0.109	0.114
NYVT	13	Mean	0.533	0.539
		SE	0.100	0.103
OR	15	Mean	0.425	0.448
		SE	0.116	0.097
SC	6	Mean	0.542	0.493
		SE	0.150	0.126
TN	500	Mean	0.528	0.581
		SE	0.095	0.106
TX	13	Mean	0.524	0.590
		SE	0.133	0.089
WI	15	Mean	0.606	0.570
		SE	0.099	0.104

**TABLE 1.**—Continued. Mean and standard error (SE) of observed and expected heterozygosity ( $H_o$  and  $H_e$ , respectively) for each population over the 8 microsatellite loci analyzed for n individual raccoons (*Procyon lotor*) that were sampled to determine genetic structuring at 3 scales across the United States and Canada.

c)

Pop.	n		$H_o$	$H_e$
AR	11	Mean	0.632	0.616
		SE	0.115	0.073
GA	5	Mean	0.369	0.528
		SE	0.125	0.082
IN	6	Mean	0.458	0.490
		SE	0.098	0.106
KYE	13	Mean	0.455	0.479
		SE	0.114	0.121
KYW	16	Mean	0.477	0.516
		SE	0.135	0.121
SC	6	Mean	0.542	0.493
		SE	0.150	0.126
TNNE	20	Mean	0.585	0.545
		SE	0.123	0.110
TNNW	21	Mean	0.593	0.540
		SE	0.119	0.116
TNSW	459	Mean	0.524	0.580
		SE	0.094	0.105

d)

Pop.	n		$H_o$	$H_e$
AC	43	Mean	0.499	0.527
		SE	0.101	0.106
D	79	Mean	0.512	0.561
		SE	0.102	0.102
H	110	Mean	0.543	0.581
		SE	0.092	0.100
M	152	Mean	0.513	0.573
		SE	0.092	0.102
MC	28	Mean	0.555	0.561
		SE	0.106	0.112
P	29	Mean	0.532	0.587
		SE	0.097	0.108

**TABLE 2.**—Mean and standard error (SE) of observed and expected heterozygosity ( $H_o$  and  $H_e$ , respectively) over the combined populations for each of the 8 microsatellite loci analyzed for raccoons (*Procyon lotor*) in a study of genetic structure at different geographic scales across the United States and Canada. a) and b): Data at the transcontinental scale analyzed by regions and states, respectively; c) Sites in the southeastern area; d) Trapping grids in southwestern Tennessee.

	Locus	G10B	G10X	PFL9	PL35	PL40	PFL11	PFL4	PL61
a)									
$H_o$	Mean	0.027	0.298	0.788	0.457	0.537	0.789	0.774	0.414
	SE	0.023	0.084	0.085	0.06	0.088	0.033	0.039	0.043
$H_e$	Mean	0.156	0.284	0.782	0.498	0.571	0.828	0.885	0.437
	SE	0.072	0.085	0.047	0.029	0.092	0.021	0.024	0.014
b)									
$H_o$	Mean	0.012	0.29	0.853	0.458	0.565	0.793	0.765	0.37
	SE	0.01	0.064	0.045	0.057	0.069	0.047	0.033	0.036
$H_e$	Mean	0.15	0.285	0.783	0.484	0.59	0.799	0.845	0.396
	SE	0.047	0.053	0.021	0.043	0.047	0.019	0.015	0.026
c)									
$H_o$	Mean	0.009	0.273	0.872	0.471	0.575	0.869	0.742	0.309
	SE	0.006	0.062	0.04	0.058	0.091	0.063	0.042	0.036
$H_e$	Mean	0.097	0.246	0.823	0.467	0.623	0.819	0.828	0.352
	SE	0.043	0.049	0.013	0.047	0.051	0.027	0.018	0.044
d)									
$H_o$	Mean	0.02	0.42	0.811	0.447	0.604	0.828	0.694	0.382
	SE	0.007	0.044	0.017	0.046	0.048	0.011	0.027	0.038
$H_e$	Mean	0.065	0.378	0.836	0.47	0.63	0.85	0.905	0.385
	SE	0.017	0.022	0.01	0.036	0.02	0.012	0.006	0.037



**TABLE 3.**—*P*-value and standard error (SE) for the global test for the alternate hypothesis of heterozygote deficit across the combined 8 microsatellite loci analyzed for each population (Pop.) of raccoons (*Procyon lotor*) sampled in a study of genetic structure at different geographic scales across the United States and Canada. Scales included: a) Transcontinental regions; the site of the population (Pop.) at NW (Northwest) included Oregon only; NMW (Northern Midwest) included Manitoba and Wisconsin; NE (Northeast) included New York and Vermont; EC (East Central) included Indiana, Kentucky, and Tennessee; SMW (Southern Midwest) included Texas, Louisiana, Arkansas, and Kansas; and SE (Southeast) included Alabama, Georgia, and South Carolina. b) Southeastern area; the sites of the populations were, respectively, Arkansas, Georgia, Indiana, eastern Kentucky, western Kentucky, South Carolina, northeastern Tennessee, northwestern Tennessee, and southwestern Tennessee. c) Trapping grids in southwestern Tennessee. Identifiers were M for the Edward J. Meeman Biological Station; and for the Ames Plantation, AC, D, H, MC, and P were grids at Afternoon Course, Dusco Place, Hancock Place, Morning Course, and Pattersonville, respectively. “\*” *P*-values indicate sites with significant ( $P \leq 0.05$ ) heterozygote deficits with 8 loci included after the Bonferroni adjustment for Type 1 error.

	Pop.	<i>P</i> -value	SE
a)	EC	0.0000*	0.0000
	NE	0.0591	0.0014
	NMW	0.0022*	0.0003
	NW	0.0878	0.0009
	SE	0.0043*	0.0004.
	SMW	0.0004*	0.0001
b)	AR	0.4078	0.0031
	GA	0.0002*	0.0000
	IN	0.0482	0.0007
	KYE	0.0341	0.0015
	KYW	0.0227	0.0009
	SC	0.7193	0.0025
	TNNE	0.8361	0.0021
	TNNW	0.9201	0.0018
	TNSW	0.0000*	0.0000
c)	AC	0.0001*	0.0000
	D	0.0002*	0.0001
	H	0.0000*	0.0000
	M	0.0000*	0.0000
	MC	0.0406	0.0021
	P	0.0000*	0.0000

**TABLE 4.**—*P*-value and standard error (SE) for the global test for the alternate hypothesis of heterozygote deficit for each of 8 microsatellite loci analyzed across combined populations of raccoons (*Procyon lotor*) sampled in a study of genetic structure at different geographic scales across the United States and Canada. a) Transcontinental populations including Alabama, Arkansas, Georgia, Indiana, Kansas, Kentucky, Louisiana, Manitoba, New York, Oregon, South Carolina, Tennessee, Texas, Vermont, and Wisconsin. b) Populations in the southeastern area comprising Arkansas, Georgia, Indiana, eastern Kentucky, western Kentucky, South Carolina, northeastern Tennessee, northwestern Tennessee, and southwestern Tennessee. c) Populations in southwestern Tennessee comprising trapping grids at the Edward J. Meeman Biological Station; and the grids at the Ames Plantation at Afternoon Course, Dusco Place, Hancock Place, Morning Course, and Pattersonville. The “\*” *P*-values indicate loci with significant ( $P \leq 0.05$ ) heterozygote deficits with all combined sites included, after the Bonferroni adjustment for Type 1 error.

	Locus	P-value	SE
a)	G10B	0.0000*	0.0000
	G10X	0.1929	0.0047
	PFL9	0.0344	0.0024
	PL35	0.1433	0.0035
	PL40	0.0049*	0.0006
	PFL11	0.0020*	0.0008
	PFL4	0.0000*	0.0000
	PL61	0.0210	0.0011
b)	G10B	0.0000*	0.0000
	G10X	0.3098	0.0075
	PFL9	0.0142	0.0012
	PL35	0.3566	0.0062
	PL40	0.0192	0.0012
	PFL11	0.0049*	0.0011
	PFL4	0.0000*	0.0000
	PL61	0.0204	0.0009
c)	G10B	0.0000*	0.0000
	G10X	0.5840	0.0032
	PFL9	0.0241	0.0013
	PL35	0.3301	0.0027
	PL40	0.0802	0.0021
	PFL11	0.0156	0.0014
	PFL4	0.0000*	0.0000
	PL61	0.0550	0.0019

**TABLE 5.**—Matrix of relationships between pairs of populations, based on 8 microsatellite loci for raccoons (*Procyon lotor*) sampled in a study of genetic structure at different geographic scales across the United States and Canada. Numbers of migrants per generation (Nm) are above the diagonal and Nei (1987) standard genetic distances ( $D_s$ ) below the diagonal. a) Transcontinental regions; for identifiers, NW (Northwest) included Oregon only; NMW (Northern Midwest) included Manitoba and Wisconsin; NE (Northeast) included New York and Vermont; EC (East Central) included Indiana, Kentucky, and Tennessee; SMW (Southern Midwest) included Texas, Louisiana, Arkansas, and Kansas; and SE (Southeast) included Alabama, Georgia, and South Carolina. b) Transcontinental states; population identifiers were state and province abbreviations for Alabama, Arkansas, Georgia, Indiana, Kansas, Kentucky, Louisiana, Manitoba, New York-Vermont, Oregon, South Carolina, Tennessee, Texas, and Wisconsin, respectively. c) Sites in the southeastern area; population identifiers were, respectively, Arkansas, Georgia, Indiana, eastern Kentucky, western Kentucky, South Carolina, northeastern Tennessee, northwestern Tennessee, and southwestern Tennessee. d) Grids in southwestern Tennessee; identifiers were M for the Edward J. Meeman Biological Station; and for the grids at the Ames Plantation, were AC, D, H, MC, and P for Afternoon Course, Dusco Place, Hancock Place, Morning Course, and Pattersonville, respectively.

a)

	EC	NE	NMW	NW	SE	SMW	
EC	--	12.25	16.17	0.98	10.45	11.41	EC
NE	0.06	--	8.58	0.89	6.22	5.57	NE
NMW	0.05	0.09	--	0.87	9.37	6.93	NMW
NW	0.67	0.75	0.76	--	0.78	1.29	NW
SE	0.06	0.11	0.07	0.86	--	5.69	SE
SMW	0.05	0.11	0.07	0.60	0.11	--	SMW
	EC	NE	NMW	NW	SE	SMW	

**TABLE 5.**—Continued. Matrix of relationships between pairs of populations, based on 8 microsatellite loci for raccoons (*Procyon lotor*) sampled in a study of genetic structure at different geographic scales across the United States and Canada.

b) Continued below

	AL	AR	GA	IN	KS	KY	LA	
AL	--	2.974	2.749	3.285	3.390	9.445	2.955	AL
AR	0.167	--	4.824	3.460	7.165	5.313	4.427	AR
GA	0.196	0.142	--	2.418	2.983	3.271	3.302	GA
IN	0.169	0.164	0.280	--	5.325	5.391	4.045	IN
KS	0.165	0.117	0.265	0.120	--	6.022	5.095	KS
KY	0.060	0.104	0.190	0.127	0.112	--	4.220	KY
LA	0.197	0.212	0.258	0.144	0.174	0.159	--	LA
MB	0.109	0.162	0.305	0.147	0.123	0.079	0.168	MB
NYVT	0.102	0.179	0.233	0.117	0.146	0.082	0.137	NYVT
OR	0.780	0.631	1.101	0.914	0.714	0.649	0.928	OR
SC	0.140	0.220	0.203	0.180	0.186	0.112	0.174	SC
TN	0.075	0.087	0.183	0.083	0.074	0.032	0.123	TN
TX	0.210	0.183	0.406	0.299	0.173	0.175	0.291	TX
WI	0.097	0.127	0.168	0.127	0.113	0.085	0.113	WI
	AL	AR	GA	IN	KS	KY	LA	

b) Continued from above

	MB	NYVT	OR	SC	TN	TX	WI	
AL	4.979	5.670	0.729	3.430	6.964	2.565	5.335	AL
AR	3.438	3.918	1.138	2.435	7.897	4.234	5.379	AR
GA	2.247	2.815	0.651	2.784	3.789	1.830	3.878	GA
IN	4.400	4.977	0.680	3.440	7.833	2.014	5.449	IN
KS	4.748	5.002	1.018	3.285	10.744	3.935	6.775	KS
KY	8.139	9.270	0.916	4.760	21.483	3.576	8.211	KY
LA	3.615	4.803	0.941	3.381	5.808	2.920	6.063	LA
MB	--	5.310	0.757	3.506	8.115	2.478	5.419	MB
NYVT	0.123	--	0.889	3.304	12.049	3.134	6.909	NYVT
OR	0.802	0.753	--	0.658	0.985	1.295	0.882	OR
SC	0.166	0.168	0.923	--	4.931	1.802	4.757	SC
TN	0.080	0.065	0.667	0.111	--	3.953	11.324	TN
TX	0.223	0.201	0.554	0.310	0.160	--	2.709	TX
WI	0.114	0.106	0.780	0.117	0.074	0.239	--	WI
	MB	NYVT	OR	SC	TN	TX	WI	

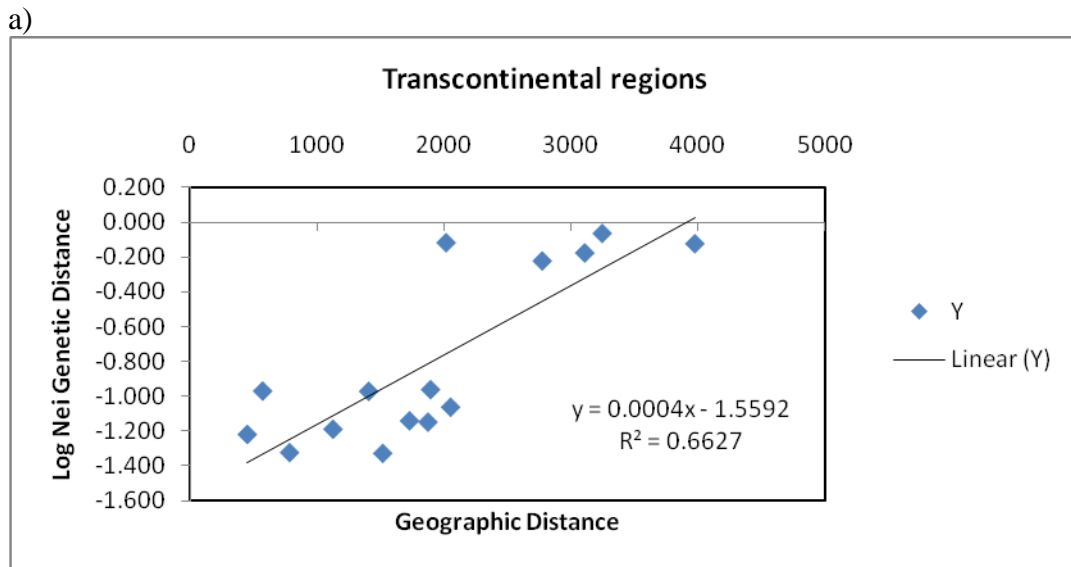
**TABLE 5.**—Continued. Matrix of relationships between pairs of populations, based on 8 microsatellite loci for raccoons (*Procyon lotor*) sampled in a study of genetic structure at different geographic scales across the United States and Canada.

c)

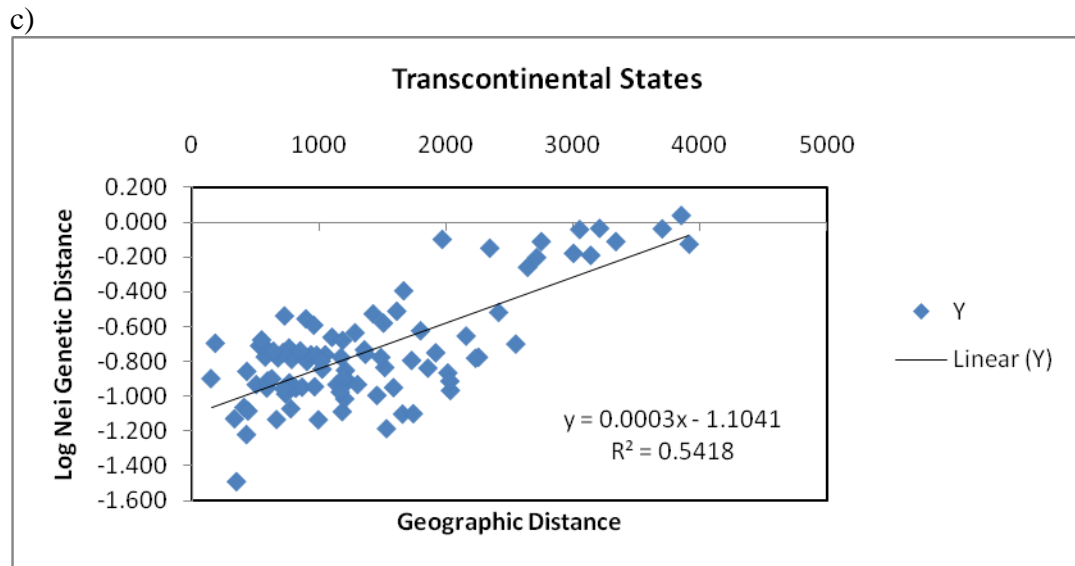
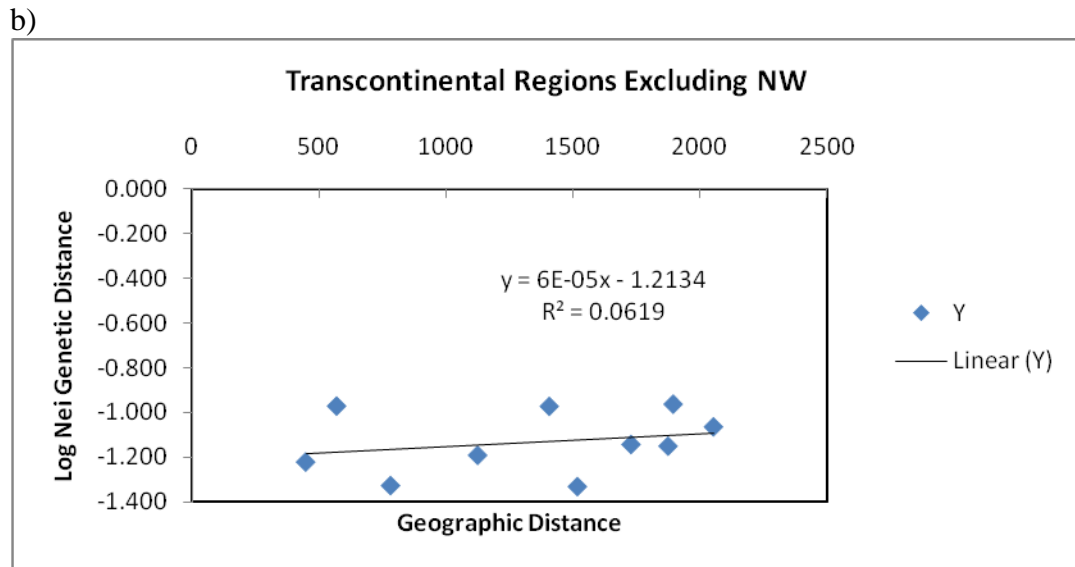
	AR	GA	IN	KYE	KYW	SC	TNNE	TNNW	TNSW
AR	--	4.82	3.46	4.28	4.49	2.44	3.14	4.35	8.11
GA	0.142	--	2.42	2.64	2.69	2.78	2.73	2.55	3.8
IN	0.164	0.28	--	4.32	4.24	3.44	5.02	4.97	7.61
KYE	0.105	0.197	0.135	--	6.91	2.97	4.45	9.42	11.55
KYW	0.131	0.246	0.148	0.087	--	3.95	6.46	10.59	10.77
SC	0.22	0.203	0.18	0.163	0.125	--	6.29	3.85	4.76
TNNE	0.219	0.272	0.155	0.148	0.097	0.104	--	6.7	7.19
TNNW	0.145	0.25	0.127	0.071	0.054	0.135	0.107	--	14.57
TNSW	0.086	0.183	0.084	0.05	0.059	0.115	0.106	0.052	--
	AR	GA	IN	KYE	KYW	SC	TNNE	TNNW	TNSW

d)

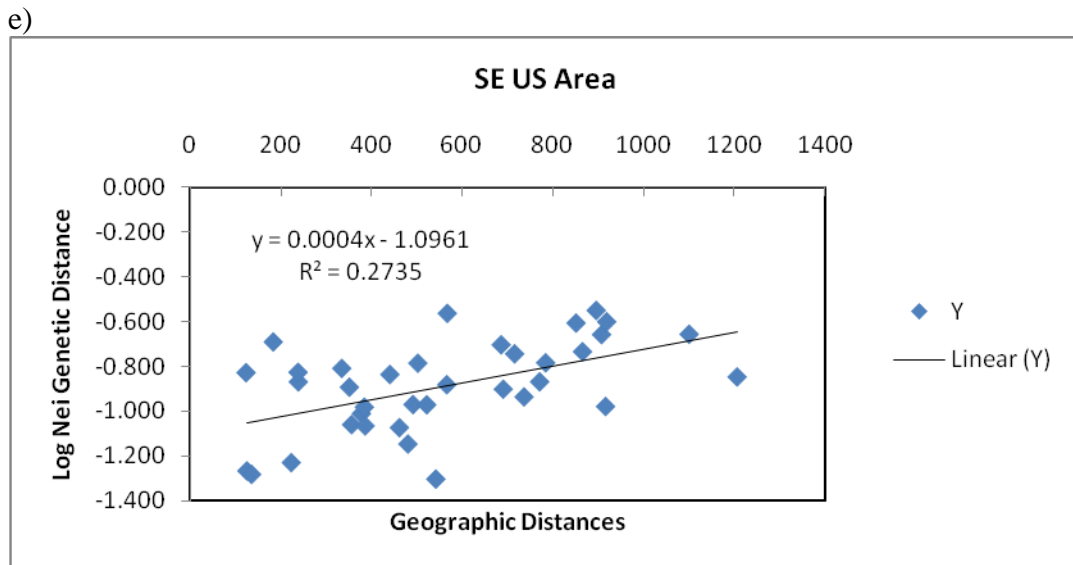
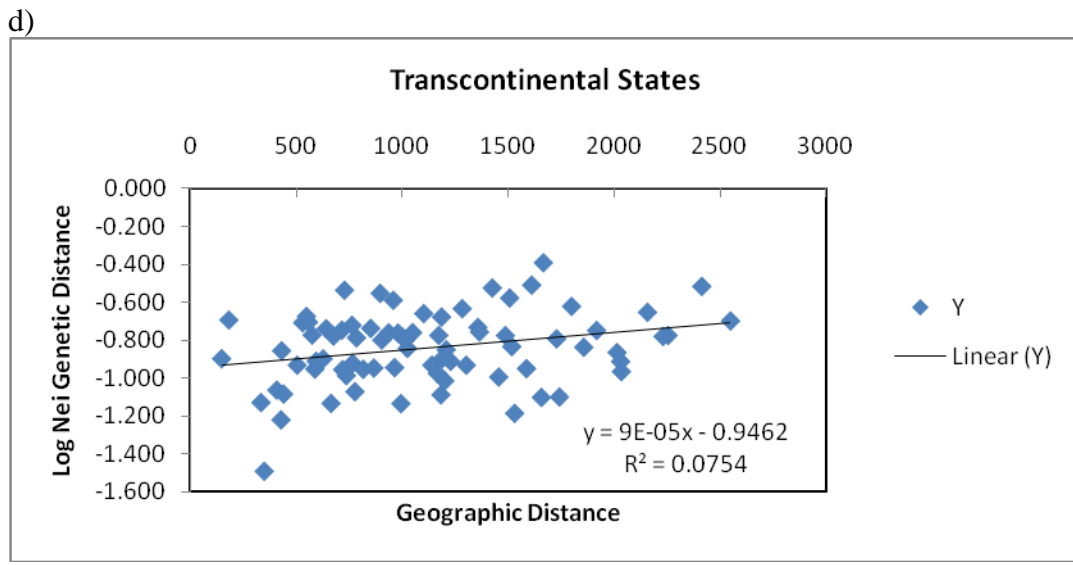
	AC	D	H	M	MC	P	
AC	--	23.20	25.99	22.60	26.18	11.44	AC
D	0.026	--	30.48	22.25	15.21	18.01	D
H	0.021	0.026	--	21.09	21.05	30.94	H
M	0.035	0.036	0.044	--	21.22	17.39	M
MC	0.025	0.039	0.031	0.038	--	14.63	MC
P	0.049	0.032	0.024	0.040	0.044	--	P
	AC	D	H	M	MC	P	



**FIG. 1.**—Continued on following pages. Plots of Mantel test correlations between geographic distance in km and log Nei genetic distance between pairs of populations based on 8 microsatellite loci for raccoons (*Procyon lotor*) sampled in a study of genetic structure at different geographic scales across the United States and Canada. a) Transcontinental regions comprising the Northwest (NW), including Oregon only; Northern Midwest, including Manitoba and Wisconsin; Northeast, including New York and Vermont; East Central, including Indiana, Kentucky, and Tennessee; Southern Midwest, including Texas, Louisiana, Arkansas, and Kansas; and Southeast, including Alabama, Georgia, and South Carolina. b) Transcontinental regions as above but excluding the Northwest region. c) Transcontinental states; these comprise the same states as used in the transcontinental regions but with distances calculated among individual states rather than among regions. d) Transcontinental states as above but excluding Oregon (NW). e) Sites in the southeastern area, comprising Arkansas, Georgia, Indiana, eastern Kentucky, western Kentucky, South Carolina, northeastern Tennessee, northwestern Tennessee, and southwestern Tennessee. f) Trapping grids in southwestern Tennessee, comprising that at the Edward J. Meeman Biological Station, and the grids at Ames Plantation at Afternoon Course, Dusco Place, Hancock Place, Morning Course, and Pattersonville. g) Trapping grids in southwestern Tennessee (SW TN) as above but excluding that at the Edward J. Meeman Biological Station (Meeman).

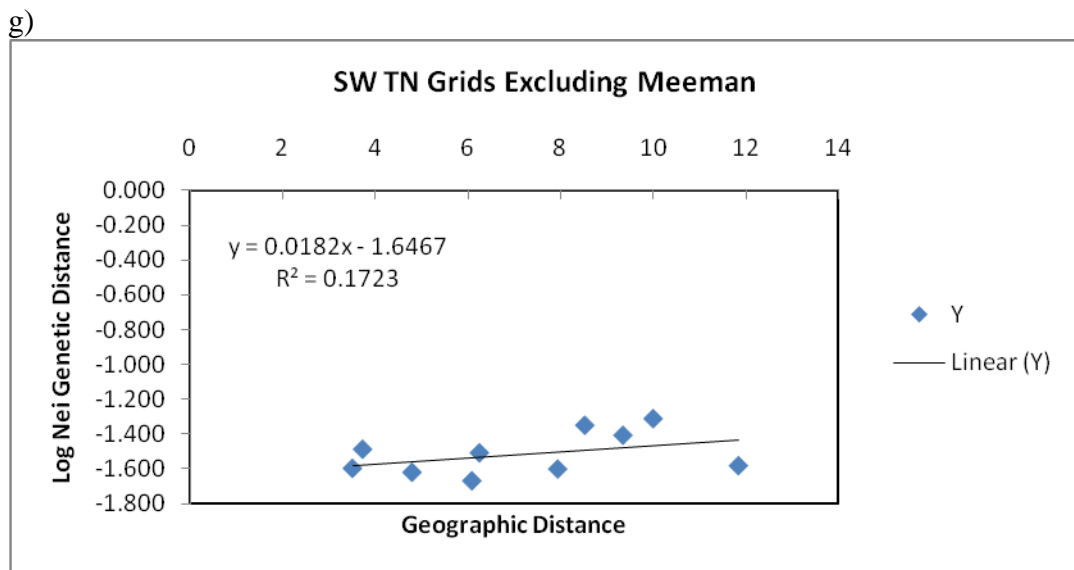
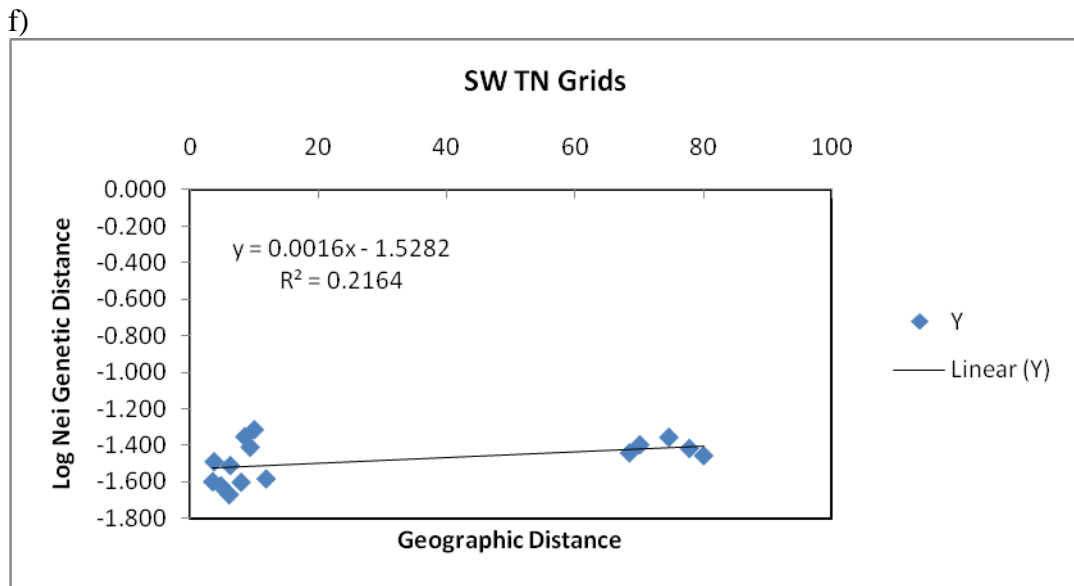


**FIG. 1.**—Continued. Plots of Mantel test correlations between geographic distance in km and log Nei genetic distance between pairs of populations based on 8 microsatellite loci for raccoons (*Procyon lotor*) sampled in a study of genetic structure at different geographic scales across the United States and Canada.



**FIG. 1.**—Continued. Plots of Mantel test correlations between geographic distance in km and log Nei genetic distance between pairs of populations based on 8 microsatellite loci for raccoons (*Procyon lotor*) sampled in a study of genetic structure at different geographic scales across the United States and Canada.





**FIG. 1.**—Continued. Plots of Mantel test correlations between geographic distance in km and log Nei genetic distance between pairs of populations based on 8 microsatellite loci for raccoons (*Procyon lotor*) sampled in a study of genetic structure at different geographic scales across the United States and Canada.

#### APPENDIX IV

Genotypes at microsatellite loci for raccoons (*Procyon lotor*) used in analyses of genetic structure at 3 geographic scales across the United States and Canada: transcontinental, southeastern area, and local southwestern Tennessee sites.

**TABLE 1.**—Locations, identification numbers, and genotypes at 9 microsatellite loci for 655 raccoons (*Procyon lotor*) used in analyses of genetic structure at 3 geographic scales across the United States and Canada: transcontinental, southeastern area, and local southwestern Tennessee sites. Site abbreviations are for Alabama (AL), Arkansas (AR), Georgia (GA), Indiana (IN), Kansas (KS), Kentucky (KY), eastern Kentucky (KYE), western Kentucky (KYW), all other Kentucky locations (KY), Louisiana (LA), Manitoba (MB), New York-Vermont (NYVT), Oregon (OR), South Carolina (SC); northeastern Tennessee (TNNE); northwestern Tennessee (TNNW); southwestern Tennessee (TNSW); Texas (TX), and Wisconsin (WI). IDs with prefixes of M-R, AC-R, D-R, H-R, MC-R, and P-R are the numbers from the right ear tags of raccoons from The Edward J. Meeman Biological Station, and the grids at the Ames Plantation at Afternoon Course, Dusco Place, Hancock Place, Morning Course, and Pattersonville, respectively. The remaining columns are the numbers of bases in the pairs of alleles for microsatellite loci G10B, G10C, G10X, Pfl4, Pfl9, Pfl11, Pl-35, Pl-40, and Pl-61. A zero in one of these columns designates an allele for which a size could not be confidently assigned.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
AL	AL-1029	159	159	103	107	152	152	233	235	220	222	160	180	279	279	175	175	133	153
AL	AL-1361	159	159	105	124	148	152	0	0	227	229	158	158	0	0	175	175	133	135
AL	AL-1362	0	0	103	109	152	152	0	0	227	231	160	162	279	279	175	188	133	155
AL	AL-1363	159	159	103	107	152	152	195	195	222	0	153	156	277	279	175	182	133	133
AL	AL-1364	159	159	113	122	152	152	225	231	218	227	166	175	279	279	176	176	133	133
AL	AL-1365	159	159	111	117	152	152	0	0	222	227	160	164	279	279	175	176	133	133
AR	AR-106	159	159	103	119	150	152	229	241	222	229	156	175	277	283	175	175	133	133
AR	AR-107	159	159	107	124	150	152	171	195	229	233	160	175	277	279	175	175	133	133
AR	AR-108	159	159	103	107	150	152	0	0	224	229	171	175	279	281	175	175	133	133
AR	AR-109	161	161	111	115	152	152	207	237	220	224	156	175	279	281	176	196	133	133
AR	AR-110	159	159	0	0	150	152	195	195	214	227	156	168	279	281	175	176	133	135
AR	AR-111	159	159	0	0	152	152	195	229	218	227	156	168	279	281	175	176	133	135
AR	AR-112	159	159	103	119	150	152	223	247	222	229	171	175	0	0	175	192	133	135
AR	AR-113	159	159	103	107	150	152	219	227	214	214	171	173	279	281	175	176	133	135

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
AR	AR-114	159	159	103	115	150	150	195	213	229	229	156	160	279	279	175	192	135	135
AR	AR-116	159	159	122	122	150	152	0	0	214	218	156	160	279	279	175	175	135	135
AR	AR-122	161	161	103	109	152	152	221	225	220	233	171	173	279	281	176	176	133	133
GA	GA-1350	159	159	109	115	152	152	0	0	212	222	158	175	279	279	175	175	135	151
GA	GA-1351	159	159	109	109	152	152	195	211	222	229	164	164	277	277	175	175	133	133
GA	GA-1352	161	161	105	115	152	152	227	237	214	224	156	156	279	279	176	176	133	133
GA	GA-1353	159	159	103	113	150	152	195	195	222	224	156	156	277	281	175	175	135	135
GA	GA-1354	159	159	109	115	152	152	239	241	216	227	156	164	277	279	175	175	135	135
IN	IN-1141	159	159	103	103	152	152	0	0	216	229	153	162	279	279	175	196	133	135
IN	IN-1142	159	159	107	107	152	152	191	0	224	229	160	177	281	281	176	176	133	147
IN	IN-1143	159	159	107	122	152	152	221	221	229	233	160	160	279	281	175	175	133	133
IN	IN-1144	159	159	107	124	152	152	219	219	218	227	160	177	279	281	175	175	133	133
IN	IN-1145	159	159	107	122	150	152	191	217	224	224	158	160	277	279	175	176	133	133
IN	IN-1146	159	159	109	113	152	152	217	233	229	229	162	175	277	281	175	188	133	133
KS	KS-1368	159	159	103	103	150	152	197	235	218	229	158	175	279	281	175	194	133	159
KS	KS-1369	159	159	107	126	150	152	195	203	214	227	173	177	279	281	175	188	133	147
KS	KS-1370	159	159	111	111	152	152	191	215	224	227	160	171	277	281	175	175	133	133
KS	KS-1371	159	159	117	122	152	157	0	0	224	229	173	175	279	279	175	201	157	157
KS	KS-1376	159	159	103	107	152	152	195	221	227	229	160	177	277	279	175	175	133	133
KS	KS-1377	159	159	107	122	150	152	197	197	214	227	173	177	279	279	175	175	133	157
KS	KS-1380	159	159	107	122	152	155	225	225	220	224	171	171	279	281	175	175	133	133
KS	KS-1382	159	159	103	107	152	152	191	225	224	227	171	171	279	279	175	188	133	133
KS	KS-1383	161	161	105	119	152	157	193	193	220	224	164	168	281	281	176	176	133	135

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
KS	KS-1384	159	159	107	115	150	152	197	203	224	227	160	173	281	281	175	175	133	133
KS	KS-1386	159	159	103	107	150	152	197	225	214	218	160	160	277	281	175	194	133	133
KS	KS-1388	159	159	103	107	150	152	203	233	214	224	171	173	279	281	175	192	133	133
KY	KY-1010	159	159	115	119	152	152	211	221	218	220	156	177	277	279	175	194	135	157
KY	KY-1012	159	159	107	124	150	152	221	231	227	233	153	171	279	279	175	186	133	135
KY	KY-1013	159	159	124	128	152	152	0	0	222	231	156	156	0	0	176	190	133	133
KY	KY-1021	159	159	105	119	152	152	195	211	220	224	156	177	277	277	194	194	133	157
KY	KY-1024	159	159	103	113	152	152	0	0	220	227	173	177	279	279	175	194	133	133
KYE	KY-1001	159	159	107	126	150	152	221	231	227	233	153	171	279	279	175	186	133	135
KYE	KY-1002	159	159	105	111	152	152	191	0	214	222	160	177	0	0	176	176	133	133
KYE	KY-1003	159	159	115	124	152	152	233	235	220	0	0	0	0	0	175	175	133	133
KYE	KY-1005	159	159	109	119	152	152	195	195	0	231	160	164	0	0	175	186	133	133
KYE	KY-1006	159	159	107	119	152	152	0	0	214	229	0	0	0	0	175	175	133	133
KYE	KY-1009	159	159	107	107	150	150	0	0	224	233	151	153	0	0	175	186	133	135
KYE	KY-1011	159	159	107	113	152	152	205	0	0	0	156	171	0	0	0	0	133	133
KYE	KY-1014	159	159	107	115	152	152	0	0	0	0	171	173	0	0	175	175	133	133
KYE	KY-1015	159	159	105	107	150	152	195	195	216	227	171	177	279	279	175	175	133	133
KYE	KY-1017	159	159	119	119	152	152	0	0	220	224	151	151	0	0	0	0	133	133
KYE	KY-1019	159	159	109	115	152	152	223	239	222	222	166	184	279	281	175	182	133	133
KYE	KY-1020	159	159	105	128	150	152	217	221	220	224	158	182	279	279	175	196	133	133
KYE	KY-1022	159	159	109	115	152	152	195	219	220	220	156	171	279	281	175	175	133	133
KYW	LBLT-1046	159	159	111	113	152	152	191	191	218	224	162	175	279	279	190	190	133	133
KYW	LBLT-1047	159	159	111	111	152	152	0	0	227	229	156	162	279	279	176	196	133	133

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
KYW	LBLT-1048	159	159	109	111	150	152	225	225	214	218	153	158	279	279	176	192	133	133
KYW	LBLT-1049	159	159	113	119	150	152	0	0	214	218	156	177	279	279	175	175	133	135
KYW	LBLT-1051	0	0	119	119	152	152	0	0	220	224	160	173	279	279	178	186	135	135
KYW	LBLT-1052	159	159	103	124	152	152	0	0	214	220	156	179	279	279	176	194	133	133
KYW	LBLT-1053	161	161	103	115	152	152	225	227	220	229	153	175	279	279	176	176	133	133
KYW	LBLT-1055	159	159	107	119	152	152	0	0	220	224	175	177	0	0	175	176	133	133
KYW	LBLT-1059	159	159	115	130	152	152	223	233	220	227	156	179	279	279	175	192	133	133
KYW	LBLT-1061	159	159	105	124	150	152	0	0	218	220	151	0	279	279	176	176	133	135
KYW	LBLT-1115	159	159	109	111	152	152	223	231	224	229	162	180	279	279	176	176	133	133
KYW	LBLT-1116	159	159	103	111	152	152	221	221	218	224	158	160	279	279	175	194	133	133
KYW	LBLT-1118	159	159	103	113	152	152	223	225	227	229	153	180	279	283	175	175	133	133
KYW	LBLT-1121	159	159	111	115	152	152	0	0	222	229	0	0	0	0	175	175	133	133
KYW	LBLT-1123	159	159	119	119	152	152	225	229	214	220	173	177	277	279	175	192	133	135
KYW	LBLT-1124	159	159	124	124	150	152	229	231	222	227	171	177	279	281	175	175	133	133
LA	LA-258	159	159	124	124	152	152	213	221	224	231	171	171	277	283	186	196	133	133
LA	LA-259	159	159	107	109	157	157	213	219	216	229	153	160	277	279	175	176	133	135
LA	LA-260	161	161	109	124	152	152	211	227	220	227	153	160	277	277	176	0	135	153
LA	LA-92	159	159	107	124	152	152	217	231	222	235	171	173	279	279	175	194	133	133
LA	LA-93	159	159	107	117	152	152	223	239	222	227	160	160	281	281	175	203	133	133
MA	MA-1096	159	159	119	124	152	152	215	225	214	214	171	171	281	281	175	176	133	133
MA	MA-1097	159	159	101	111	152	152	201	233	214	227	169	171	279	279	175	178	133	149
MA	MA-1098	159	159	101	103	152	152	0	241	214	227	153	177	279	281	178	192	133	133
MA	MA-1099	159	159	103	109	152	152	231	237	214	220	153	171	279	279	175	176	133	149

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
MA	MA-1100	159	159	105	124	152	152	239	241	214	220	160	171	279	281	175	176	133	133
MA	MA-1101	159	159	109	117	152	152	201	225	227	227	153	155	276	279	175	175	133	135
MA	MA-1102	159	159	109	109	152	152	197	197	220	229	153	179	279	279	176	176	133	133
MA	MA-1103	159	159	105	109	152	152	215	225	227	229	160	160	279	281	186	186	133	133
MA	MA-1104	159	159	111	124	150	152	225	241	214	229	160	160	279	279	175	175	133	137
MA	MA-1105	159	159	105	105	152	152	225	241	214	229	160	160	279	279	175	176	133	149
MA	MA-1106	159	159	103	109	152	152	201	215	220	227	153	171	279	279	175	176	133	133
MA	MA-1107	159	159	117	126	152	152	227	227	224	227	175	177	279	279	175	176	133	133
MA	MA-1109	159	159	115	124	152	152	197	197	220	227	171	175	279	279	176	178	133	149
MA	MA-1110	159	159	103	109	150	152	201	237	227	229	160	160	281	281	176	176	133	137
MA	MA-1113	159	159	105	115	152	152	219	231	214	220	171	171	279	279	178	178	133	149
NYVT	NY-1086	159	159	0	0	152	152	219	233	222	224	160	177	279	279	175	176	133	135
NYVT	NY-1087	159	159	124	124	152	152	227	227	210	227	160	160	277	279	190	194	133	133
NYVT	NY-1088	159	159	122	124	150	152	219	0	216	224	155	160	279	279	176	192	133	133
NYVT	NY-1089	159	159	124	124	152	152	191	191	224	229	153	155	279	279	175	182	133	151
NYVT	NY-1090	159	159	105	105	152	152	0	0	227	229	160	160	279	281	0	0	133	135
NYVT	NY-1091	159	159	105	124	152	152	215	233	222	224	160	171	279	279	175	188	133	133
NYVT	NY-1092	159	159	105	124	152	152	219	233	222	222	160	177	279	279	175	176	133	133
NYVT	NY-1093	159	159	124	124	152	157	191	223	216	224	160	177	279	279	175	175	133	151
NYVT	NY-1094	159	159	105	109	152	157	231	233	222	222	153	155	277	279	175	196	133	133
NYVT	NY-1393	159	159	109	113	152	157	0	0	0	0	164	177	0	0	0	0	133	135
NYVT	NY-1394	159	159	105	111	150	152	231	239	216	222	151	160	279	279	175	175	133	155
NYVT	VT-1391	159	159	109	115	152	152	0	0	222	222	155	160	0	0	186	186	133	133

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
NYVT	VT-1392	159	159	109	115	152	157	193	193	224	233	156	171	281	281	175	176	133	135
OR	OR-26	161	161	103	103	150	150	229	231	218	218	179	179	279	283	182	182	133	133
OR	OR-27	159	159	092	103	150	150	231	233	212	218	169	169	279	283	182	182	133	139
OR	OR-28	159	0	092	103	150	150	229	231	218	218	175	177	279	279	182	182	139	139
OR	OR-29	159	159	092	092	150	150	229	231	212	212	169	169	279	283	182	182	133	139
OR	OR-31	159	159	092	103	150	150	0	0	212	212	169	171	283	283	182	182	133	133
OR	OR-32	159	161	103	103	150	150	231	235	218	218	171	179	279	279	182	182	133	139
OR	OR-35	161	161	103	103	150	150	233	237	212	220	171	177	279	283	182	190	133	139
OR	OR-37	159	159	103	103	150	150	229	233	212	218	173	179	279	279	182	182	133	133
OR	OR-38	159	159	103	103	150	150	287	287	212	212	171	177	279	283	182	182	133	133
OR	OR-39	159	161	092	103	150	150	231	235	212	212	171	179	279	279	182	190	133	133
OR	OR-40	159	159	103	103	150	150	0	0	218	218	171	177	279	281	182	182	133	139
OR	OR-47	161	161	092	103	150	150	229	231	218	218	177	179	279	283	182	182	139	139
OR	OR-48	159	159	103	103	150	150	235	237	212	220	169	179	279	283	182	182	133	133
OR	OR-49	159	159	103	103	150	150	231	235	212	218	171	179	279	283	182	182	133	139
OR	OR-51	159	159	103	105	150	150	229	231	212	218	179	179	279	283	182	182	133	133
SC	SC-1355	159	159	105	124	152	152	225	271	220	227	153	162	277	279	175	198	133	133
SC	SC-1356	159	159	103	109	152	152	225	227	216	227	156	164	279	279	188	198	133	133
SC	SC-1357	159	159	122	124	152	152	227	229	214	224	160	166	277	277	175	175	133	133
SC	SC-1358	159	159	103	122	152	152	223	225	216	227	156	182	277	279	175	188	133	133
SC	SC-1359	159	159	107	109	152	152	229	229	229	231	158	177	277	277	175	190	133	149
SC	SC-1360	159	159	124	124	152	152	229	233	214	216	155	156	279	279	175	192	133	135
TNNE	CS-1148	159	159	109	113	152	152	0	0	227	229	153	160	0	0	175	186	133	157



TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNNE	CS-1149	159	159	111	113	152	152	0	0	0	0	153	155	0	0	175	182	133	155
TNNE	CS-1150	0	0	0	0	152	152	225	225	227	231	153	177	0	0	182	192	133	155
TNNE	CS-1151	159	179	107	119	152	152	0	0	224	227	0	0	277	281	182	186	133	157
TNNE	CS-1152	159	159	109	111	150	152	0	0	0	0	156	160	0	0	0	0	133	133
TNNE	CS-1153	159	159	107	107	150	152	203	231	224	227	153	155	279	279	188	194	133	133
TNNE	CS-1154	159	159	107	122	152	152	0	0	227	229	160	173	277	279	176	176	147	157
TNNE	CS-1156	159	159	113	119	152	152	0	0	227	231	160	166	0	0	175	176	0	0
TNNE	CS-1158	159	159	0	0	152	155	0	0	0	0	156	160	0	0	175	190	133	133
TNNE	CS-1165	159	159	107	107	152	152	0	0	227	229	153	175	0	0	175	186	133	133
TNNE	CS-1167	159	159	115	119	152	152	0	0	220	0	153	156	0	0	176	176	133	133
TNNE	CS-1168	159	159	103	111	152	152	203	229	216	229	151	156	279	279	188	194	133	133
TNNE	CS-1169	0	0	107	124	152	152	195	0	224	227	153	156	0	0	175	0	133	157
TNNE	CS-1170	159	159	107	115	152	152	0	0	224	231	0	0	0	0	0	0	133	147
TNNE	CS-1171	159	159	103	119	152	152	0	0	222	229	153	177	0	0	175	194	133	133
TNNE	CS-1173	159	159	0	0	152	152	0	0	227	229	0	0	279	0	175	192	133	133
TNNE	CS-1174	159	159	103	122	152	152	0	0	222	227	153	160	0	0	175	194	133	157
TNNE	CS-1175	159	159	109	119	152	152	0	0	0	0	151	155	0	0	0	0	133	133
TNNE	CS-1176	159	159	105	107	152	152	211	231	216	216	151	156	0	0	176	186	133	133
TNNE	CS-1177	159	159	0	0	152	152	0	0	224	229	153	153	0	0	175	182	133	155
TNNW	RLGI-1181	159	159	103	119	152	152	223	223	229	229	160	173	279	279	175	192	133	135
TNNW	RLGI-1188	159	159	107	115	152	157	0	0	218	233	160	177	279	279	175	192	133	133
TNNW	RLGI-1193	159	159	105	109	152	152	0	0	214	229	151	162	279	279	0	0	133	133
TNNW	RLGI-1194	159	159	115	115	152	157	0	0	229	231	171	173	0	0	175	0	133	133

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNNW	RLGI-1196	159	159	103	117	150	152	223	235	210	227	153	162	279	281	175	192	133	135
TNNW	RLGI-1198	159	159	105	119	152	152	0	0	218	224	156	158	0	0	0	0	133	133
TNNW	RLGI-1199	159	159	103	109	150	152	0	0	218	220	156	158	279	281	0	0	133	133
TNNW	RLGI-1204	159	159	115	0	152	152	223	231	227	233	156	177	279	279	0	0	133	135
TNNW	RLGI-1218	159	159	115	119	152	152	0	0	210	218	160	173	0	0	0	0	133	133
TNNW	RLGI-1224	159	159	107	113	152	152	215	221	214	231	158	177	279	281	175	175	133	135
TNNW	RLGI-1229	159	159	119	119	150	152	217	223	220	224	156	158	277	279	175	175	133	133
TNNW	RLGI-1286	159	159	109	119	152	152	0	0	216	224	158	177	279	279	175	192	133	135
TNNW	RLLP-1180	159	159	109	119	150	152	229	231	224	224	158	164	0	0	175	182	133	133
TNNW	RLLP-1187	159	159	103	109	152	152	215	225	214	229	151	160	279	281	186	190	133	133
TNNW	RLLP-1202	159	159	111	119	152	152	0	0	218	224	156	156	279	281	182	186	133	133
TNNW	RLLP-1208	159	159	103	119	152	152	0	0	220	224	160	173	0	0	0	0	133	137
TNNW	RLLP-1211	159	159	109	119	152	152	0	0	218	224	156	158	279	279	175	192	133	133
TNNW	RLLP-1212	159	159	111	0	152	152	0	0	224	224	156	177	279	281	175	194	133	133
TNNW	RLLP-1213	159	159	113	124	150	152	217	237	227	233	153	177	279	279	175	186	133	133
TNNW	RLLP-1214	159	159	111	115	150	152	225	235	218	227	156	158	0	0	182	186	133	133
TNNW	RLLP-1216	159	159	115	119	152	157	221	231	224	231	177	177	279	279	176	186	133	147
TNSW	AC-R6301	159	159	109	124	150	152	237	245	220	220	153	175	277	279	175	176	133	133
TNSW	AC-R6406	159	159	107	115	152	152	195	195	224	229	156	156	279	279	175	175	133	133
TNSW	AC-R6416	159	159	107	109	150	152	237	241	216	227	173	177	279	279	175	178	133	133
TNSW	AC-R806	159	159	107	115	150	152	223	225	216	229	162	175	279	279	175	178	133	135
TNSW	AC-R808	159	159	115	122	152	152	213	213	227	229	160	171	277	279	175	175	133	133
TNSW	AC-R816	159	159	103	119	150	150	197	197	229	229	160	160	277	279	175	175	133	135

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNSW	AC-R820	159	159	103	122	150	152	219	233	220	220	156	160	279	279	175	175	133	133
TNSW	AC-R822	159	159	122	124	152	152	213	215	227	229	160	166	277	279	182	190	133	133
TNSW	AC-R824	159	159	113	115	152	152	227	237	220	220	153	160	279	279	175	194	133	133
TNSW	AC-R826	159	159	103	111	150	152	195	227	214	216	160	0	279	279	175	176	133	133
TNSW	AC-R870	159	159	111	119	150	152	237	239	210	224	153	158	279	281	0	0	133	133
TNSW	AC-R881	161	161	115	122	152	152	213	215	227	229	160	171	279	279	175	175	133	135
TNSW	AC-R897	159	159	115	122	152	152	219	239	224	229	153	158	279	279	175	194	133	133
TNSW	AC-R898	159	159	109	119	150	152	223	227	224	227	158	158	279	279	190	194	133	133
TNSW	AC-R900	159	159	107	119	150	152	227	233	220	224	158	160	279	279	175	178	133	133
TNSW	AC-RA192	159	159	103	103	150	152	213	213	220	227	160	175	279	279	175	190	133	133
TNSW	AC-RA199	159	159	109	109	150	152	195	195	229	229	171	171	277	279	194	196	133	135
TNSW	AC-RA223	159	159	111	111	152	152	207	0	220	229	156	160	279	279	175	182	133	133
TNSW	AC-RA235	159	159	119	122	150	152	227	239	210	224	158	173	279	281	175	194	133	133
TNSW	AC-RA306	159	159	103	126	150	152	0	0	0	0	153	158	0	0	175	182	133	133
TNSW	AC-RA315	159	159	119	124	152	152	231	233	218	227	153	158	279	281	175	175	133	135
TNSW	AC-RA318	159	159	109	111	152	152	0	0	220	229	160	169	0	0	175	175	133	133
TNSW	AC-RA391	161	161	111	115	152	152	213	213	214	227	160	160	279	279	176	176	133	133
TNSW	AC-RA395	159	159	115	128	152	152	227	237	220	224	158	160	279	279	175	198	133	133
TNSW	AC-RA71	159	159	119	124	150	150	229	231	220	229	151	156	279	283	178	178	133	133
TNSW	AC-RA72	159	159	109	109	150	152	195	195	214	224	0	175	279	279	175	175	135	135
TNSW	AC-RA74	159	159	115	119	152	152	219	231	220	227	158	160	279	281	175	175	133	155
TNSW	AC-RA80	159	159	115	119	150	152	213	227	220	224	158	173	279	281	175	175	133	135
TNSW	AC-RA82	159	159	119	124	150	152	223	239	210	220	156	173	279	281	175	194	133	133

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNSW	AC-RA84	159	159	105	124	152	152	231	233	214	227	153	173	279	279	175	175	133	135
TNSW	AC-RA863	159	159	107	115	152	152	213	213	220	229	156	160	279	279	175	175	133	133
TNSW	AC-RA88	159	159	111	119	150	152	0	0	210	224	153	158	279	281	175	194	133	133
TNSW	AC-RA90	159	159	115	122	152	152	213	239	220	224	158	173	279	279	175	194	133	135
TNSW	AC-RA94	159	159	107	115	0	0	223	223	216	229	162	166	279	279	175	175	133	133
TNSW	AC-RA96	159	159	113	119	152	152	223	227	220	224	158	160	279	279	175	194	133	133
TNSW	AC-RA98	159	159	103	124	150	152	227	227	218	233	156	171	277	279	175	178	133	133
TNSW	AC-RUM828	159	159	109	111	152	152	227	237	229	229	158	173	279	281	175	178	133	133
TNSW	AC-RUM831	159	159	115	124	152	152	227	227	214	229	160	173	279	279	175	178	133	135
TNSW	AC-RUM833	159	159	115	115	152	152	219	223	218	224	160	162	279	279	175	175	133	133
TNSW	AC-RUM868	159	159	113	115	152	152	0	233	220	220	153	160	279	279	175	194	133	133
TNSW	AC-RUM883	159	159	111	122	152	157	195	195	224	224	158	160	279	281	175	175	133	133
TNSW	AC-RUM888	159	159	115	115	152	152	227	237	220	220	153	160	279	279	175	194	133	133
TNSW	AC-RUM890	159	159	119	122	152	152	215	233	218	224	158	158	279	281	175	175	133	135
TNSW	D-R129	159	159	105	105	150	152	213	213	220	229	153	156	279	279	176	194	133	133
TNSW	D-R163	159	159	109	109	152	152	227	227	224	233	158	160	279	279	175	182	133	135
TNSW	D-R176	159	159	103	124	150	152	235	237	224	227	160	173	277	283	175	182	133	133
TNSW	D-R177	159	159	115	124	152	152	231	0	220	222	160	173	281	281	175	175	133	151
TNSW	D-R178	159	159	115	124	152	152	0	0	222	0	151	156	0	0	0	0	133	133
TNSW	D-R180	159	159	0	0	152	152	227	237	220	224	0	0	279	279	175	175	133	133
TNSW	D-R184	159	159	103	124	152	152	197	197	220	231	160	166	277	279	175	176	133	133
TNSW	D-R186	159	159	105	124	152	152	223	233	216	216	156	160	279	281	175	175	133	133

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNSW	D-R187	157	159	103	124	152	152	215	227	214	229	0	173	279	279	175	176	133	133
TNSW	D-R188	0	0	122	124	152	155	0	0	214	222	173	173	0	0	0	0	133	135
TNSW	D-R195	159	159	111	119	150	152	213	213	220	220	153	156	279	279	175	175	133	133
TNSW	D-R28	159	159	103	107	152	152	197	237	220	220	162	177	279	281	176	176	133	133
TNSW	D-R299	159	159	115	115	152	152	221	227	224	229	162	173	277	279	175	175	133	133
TNSW	D-R32	159	159	115	124	152	152	231	237	220	227	160	177	279	281	175	182	133	151
TNSW	D-R360	159	159	103	109	152	152	0	0	222	224	160	171	277	283	182	192	135	135
TNSW	D-R41	159	159	115	122	152	152	201	203	222	229	151	173	277	279	175	175	133	135
TNSW	D-R43	159	159	109	124	152	152	227	227	227	231	156	166	277	281	175	175	133	135
TNSW	D-R45	159	159	111	128	152	152	227	237	224	224	153	173	279	279	175	176	133	133
TNSW	D-R46	159	159	115	124	150	152	215	233	227	229	160	177	279	279	175	178	151	155
TNSW	D-R482	159	159	107	115	150	152	0	0	220	224	173	173	279	283	175	194	133	133
TNSW	D-R572	159	168	107	111	152	152	213	213	0	229	160	173	277	281	175	175	133	135
TNSW	D-R582	159	159	105	107	152	152	221	225	227	229	160	179	279	279	175	194	133	135
TNSW	D-R590	159	159	128	128	152	152	215	237	224	231	153	160	279	279	175	175	133	133
TNSW	D-R6185	159	159	105	115	152	152	0	0	224	229	160	173	279	279	194	198	133	133
TNSW	D-R6190	159	159	103	122	152	152	197	221	220	224	156	160	279	279	175	175	135	135
TNSW	D-R6192	0	159	103	124	150	152	0	0	0	0	153	173	0	0	0	0	133	133
TNSW	D-R6377	157	159	105	126	152	152	213	227	218	229	173	175	277	279	175	175	133	133
TNSW	D-R6381	159	159	107	0	152	152	213	213	220	224	160	160	279	279	175	175	133	133
TNSW	D-R6382	159	159	109	119	150	150	213	219	222	222	162	175	277	281	175	192	133	135
TNSW	D-R6394	159	159	107	124	152	152	195	215	222	227	153	156	279	279	175	175	133	135

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNSW	D-R6400	159	159	107	117	152	152	231	233	210	216	175	177	279	279	175	175	133	133
TNSW	D-R6413	159	159	109	119	152	152	227	237	216	231	158	166	279	281	175	175	133	135
TNSW	D-R6420	159	159	107	119	152	152	213	213	220	224	160	160	279	279	175	175	133	133
TNSW	D-R6477	161	161	103	122	152	152	221	229	220	224	156	160	279	279	176	176	135	135
TNSW	D-R6478	159	159	109	115	150	152	195	227	224	224	160	175	279	281	175	175	133	135
TNSW	D-R6482	0	0	103	111	150	152	215	227	224	229	156	0	279	279	175	176	133	133
TNSW	D-R6484	159	159	107	117	152	152	231	233	210	216	175	177	279	279	176	176	133	133
TNSW	D-R6488	159	159	107	122	152	152	203	205	220	220	160	173	279	283	182	194	133	133
TNSW	D-R6490	161	161	103	107	152	152	231	237	220	227	160	177	279	279	176	184	133	151
TNSW	D-R6492	159	159	109	124	150	152	229	241	224	224	156	160	277	277	175	175	133	135
TNSW	D-R6494	159	159	107	111	152	152	201	215	220	220	160	173	277	279	175	190	133	135
TNSW	D-R6496	157	157	103	111	152	152	215	215	224	229	156	173	279	279	175	176	133	133
TNSW	D-R6498	159	159	111	122	152	152	213	233	214	220	160	160	279	279	175	190	133	133
TNSW	D-R964	159	159	103	109	150	157	213	213	222	224	162	175	277	279	175	175	133	135
TNSW	D-R966	159	159	105	122	150	152	197	197	220	220	0	160	279	281	175	175	133	133
TNSW	D-R998	159	159	107	115	152	152	0	0	224	224	155	160	277	281	175	190	149	151
TNSW	D-RA245	159	159	109	122	152	152	227	227	224	224	175	177	277	281	175	192	133	135
TNSW	D-RA612	159	159	103	105	150	152	213	225	227	227	153	173	279	279	175	182	133	135
TNSW	D-RA618	159	159	107	109	152	152	221	233	220	224	162	177	277	281	175	175	133	149
TNSW	D-RA627	159	159	103	115	150	150	227	237	218	220	160	160	279	279	175	175	133	133
TNSW	D-RA635	159	159	119	124	152	152	227	229	216	227	160	166	279	279	175	188	133	133
TNSW	D-RA637	159	159	124	124	152	152	215	227	222	231	160	171	279	279	175	176	133	135

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNSW	D-RA639	159	159	124	124	152	152	195	225	229	231	162	0	279	279	175	194	133	133
TNSW	D-RA641	159	159	109	124	152	152	213	219	227	229	156	177	279	279	175	175	133	135
TNSW	D-RUM1	159	159	0	0	150	152	227	235	218	220	153	160	279	279	175	175	133	135
TNSW	D-RUM10	159	159	103	115	152	152	223	225	216	227	160	166	279	279	175	176	133	135
TNSW	D-RUM12	0	0	115	128	152	152	201	215	0	0	0	0	279	279	175	175	133	133
TNSW	D-RUM14	159	159	107	107	152	152	195	229	229	0	160	160	279	279	188	196	133	151
TNSW	D-RUM17	159	159	105	105	152	157	231	237	220	233	160	171	277	279	175	190	133	135
TNSW	D-RUM313	159	159	119	124	150	152	219	233	222	229	156	175	277	277	175	175	133	135
TNSW	D-RUM33	159	159	111	115	152	152	219	233	224	229	156	166	279	279	182	188	133	135
TNSW	D-RUM4	159	159	115	115	152	152	201	237	216	224	160	173	279	279	175	194	133	135
TNSW	D-RUM508	159	159	115	119	152	152	0	0	222	229	158	173	279	279	175	198	133	133
TNSW	D-RUM509	159	159	119	124	150	157	213	215	218	220	153	177	279	279	175	175	133	133
TNSW	D-RUM513	159	159	119	119	152	152	237	239	216	231	166	166	279	279	175	196	133	135
TNSW	D-RUM514	159	159	111	115	152	152	0	0	224	224	162	175	279	279	175	175	133	135
TNSW	D-RUM517	159	159	115	119	152	152	227	227	220	229	156	158	279	279	194	198	133	133
TNSW	D-RUM520	159	159	111	115	152	152	227	227	222	224	151	156	277	279	175	175	133	133
TNSW	D-RUM561	159	159	103	111	150	152	213	219	224	229	156	173	279	281	178	182	133	133
TNSW	D-RUM562	0	0	128	128	152	152	215	237	224	231	153	160	279	279	176	176	133	133
TNSW	D-RUM563	159	159	115	115	150	152	227	229	216	222	156	184	279	279	175	194	133	135
TNSW	D-RUM571	159	159	119	128	152	152	215	227	220	231	160	160	279	279	175	194	133	133
TNSW	D-RUM577	159	159	109	111	150	152	215	227	220	231	156	156	277	279	175	198	133	133
TNSW	D-RUM579	159	159	115	119	152	152	225	225	222	222	160	166	279	279	194	194	133	133

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNSW	D-RUM585	159	159	111	124	152	152	195	215	216	224	156	175	281	281	175	176	133	133
TNSW	D-RUM591	159	159	115	122	152	152	201	227	220	229	0	158	279	279	175	198	133	135
TNSW	D-RUM592	159	159	111	115	152	152	201	227	222	224	156	173	279	279	175	175	133	135
TNSW	D-RUM6	159	159	103	105	152	152	215	237	224	229	0	160	279	281	175	175	133	135
TNSW	D-RUM8	159	159	109	126	152	152	219	237	220	229	160	175	279	281	175	194	133	135
TNSW	HA-1334	159	159	115	119	152	152	195	195	218	229	153	164	277	279	175	175	133	155
TNSW	HA-1335	159	159	115	124	152	152	231	243	222	224	160	171	279	279	175	196	133	133
TNSW	HA-1336	159	159	103	119	152	152	195	195	224	229	153	160	277	279	178	194	133	135
TNSW	HA-1337	159	159	103	119	152	152	179	195	214	220	153	160	0	0	194	194	133	133
TNSW	HA-1338	159	159	115	124	152	152	0	0	214	224	153	160	279	279	175	186	133	133
TNSW	HA-1339	159	159	113	124	152	152	217	227	222	224	160	177	279	279	175	175	133	133
TNSW	HA-1340	159	159	119	119	152	152	0	237	220	227	153	160	279	281	175	0	133	133
TNSW	HA-1341	159	159	109	115	150	152	0	0	218	224	160	173	279	281	175	184	133	135
TNSW	HA-1342	159	159	115	115	152	152	239	243	220	220	162	173	279	279	0	0	133	135
TNSW	HA-1343	159	159	111	119	150	152	0	0	216	229	160	164	0	0	175	0	151	155
TNSW	HA-1344	159	159	113	124	152	152	213	213	227	227	156	0	279	279	175	176	135	135
TNSW	HA-1345	159	159	109	109	150	152	0	0	214	224	160	177	279	281	175	175	133	133
TNSW	HA-1346	159	159	115	124	0	152	195	221	214	224	153	153	0	0	175	186	133	137
TNSW	HA-5001	159	159	105	109	150	150	201	237	216	222	153	160	277	279	175	175	133	135
TNSW	HA-5002	159	159	113	124	150	152	0	0	218	229	156	177	277	279	175	175	133	151
TNSW	HA-5004	159	159	109	124	152	152	0	0	214	222	153	160	279	281	175	175	133	135
TNSW	HA-5006	159	159	109	124	152	152	221	231	214	218	166	169	279	281	176	176	133	135



TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNSW	HA-5016	159	159	115	115	152	152	227	231	220	229	156	173	279	281	186	196	133	133
TNSW	H-cub	159	159	119	119	150	152	195	195	222	227	166	0	277	279	175	196	133	135
TNSW	H-parent	159	159	107	119	150	152	195	195	220	227	0	0	277	281	175	175	133	133
TNSW	H-R301	159	159	103	111	152	152	231	233	220	224	158	160	279	279	175	176	133	135
TNSW	H-R302	159	159	103	103	150	152	0	0	218	220	169	173	0	0	178	194	133	133
TNSW	H-R305	159	159	109	115	150	152	219	237	220	220	160	160	279	279	176	182	133	133
TNSW	H-R326	159	159	107	111	150	152	0	0	222	224	171	171	279	279	175	175	133	135
TNSW	H-R327	159	159	109	119	150	152	0	0	220	229	166	175	0	0	0	0	135	135
TNSW	H-R329	159	159	103	119	152	152	0	0	216	222	153	160	279	279	175	175	133	135
TNSW	H-R331	159	159	103	103	150	152	225	227	220	220	160	171	277	281	176	178	133	133
TNSW	H-R332	159	159	103	107	152	152	227	237	218	222	147	158	277	279	176	194	133	135
TNSW	H-R339	159	159	103	103	152	152	195	195	220	227	160	175	0	0	175	175	135	135
TNSW	H-R347	159	159	105	124	152	152	201	241	214	220	158	160	279	281	175	176	133	135
TNSW	H-R349	159	159	115	119	150	152	0	0	216	224	156	162	279	279	175	175	133	133
TNSW	H-R352	159	159	111	119	150	152	235	237	222	227	171	177	277	279	175	175	133	133
TNSW	H-R371	159	159	109	128	152	157	219	237	220	229	171	173	279	279	175	175	133	133
TNSW	H-R373	159	159	107	109	152	152	0	0	216	220	160	162	279	279	175	0	133	133
TNSW	H-R449	159	159	103	105	150	152	195	195	218	224	153	160	279	279	175	194	135	135
TNSW	H-R630	159	159	105	113	152	152	213	225	224	229	158	173	279	279	175	182	133	135
TNSW	H-R632	159	159	109	113	152	152	219	227	220	220	156	162	279	279	175	192	133	133
TNSW	H-R634	159	159	103	107	150	152	195	239	220	224	158	173	277	279	175	194	133	135
TNSW	H-R635	159	159	103	113	150	152	219	221	210	220	153	162	279	281	175	186	133	133
TNSW	H-R638	159	159	105	109	152	152	201	227	220	220	156	160	279	279	175	192	133	135

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNSW	H-R640	159	159	109	122	152	152	213	233	220	227	156	166	279	279	175	175	133	135
TNSW	H-R642	159	159	103	115	152	152	213	213	220	220	158	177	279	281	175	194	135	149
TNSW	H-R644	159	159	105	119	150	152	201	213	229	229	156	166	279	281	175	175	133	135
TNSW	H-R648	159	159	103	103	150	152	223	225	216	229	166	184	277	279	175	175	129	133
TNSW	H-R701	159	159	105	107	150	152	235	237	224	224	156	0	279	279	175	194	133	133
TNSW	H-R703	159	159	107	124	152	152	227	231	224	227	160	175	277	281	175	196	133	135
TNSW	H-R706	159	159	119	124	150	152	195	195	220	224	169	169	277	279	194	196	133	133
TNSW	H-R707	159	159	103	103	152	152	219	245	224	227	153	173	281	281	175	190	133	133
TNSW	H-R712	159	159	107	119	150	152	195	0	220	227	169	169	277	281	175	175	133	133
TNSW	H-R725	159	159	107	107	150	152	227	231	224	229	171	171	277	279	175	175	133	133
TNSW	H-R726	159	159	105	124	152	152	0	0	220	229	158	173	279	279	175	190	133	133
TNSW	H-R728	159	159	103	107	152	152	227	237	220	224	158	160	279	281	175	175	133	149
TNSW	H-R730	159	159	103	124	150	150	195	221	220	229	0	173	277	279	175	194	133	133
TNSW	H-R732	159	159	103	109	152	152	229	231	210	224	160	171	279	281	175	194	133	133
TNSW	H-R735	159	159	103	107	152	152	217	217	218	222	147	158	279	279	176	176	133	135
TNSW	H-R736	159	159	115	124	152	152	213	227	220	229	160	177	277	281	175	194	133	135
TNSW	H-R738	159	159	105	115	152	152	195	195	220	224	0	0	279	279	175	175	0	0
TNSW	H-R740	159	159	107	124	150	152	221	231	220	220	160	173	277	279	175	175	133	133
TNSW	H-R742	159	159	115	119	152	152	213	227	222	229	153	173	279	279	175	182	133	133
TNSW	H-R744	159	159	103	124	150	152	213	225	220	220	158	173	277	281	175	178	133	133
TNSW	H-R746	159	159	119	119	152	152	233	233	222	229	166	166	279	281	196	196	133	135
TNSW	H-R748	159	0	105	119	152	152	195	213	0	0	158	169	279	281	182	196	133	133
TNSW	H-R750	159	159	109	124	152	152	0	0	216	220	156	169	279	279	175	175	133	133

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNSW	H-R751	159	159	124	124	150	152	195	195	216	220	0	0	279	279	175	175	133	133
TNSW	H-R757	159	159	119	124	152	152	195	195	220	227	158	158	279	281	175	196	133	133
TNSW	H-R759	159	159	105	107	150	152	195	237	224	227	156	173	277	279	175	182	133	133
TNSW	H-R762	159	159	105	122	152	152	215	227	0	0	153	168	279	279	0	0	133	135
TNSW	H-R765	159	159	115	119	152	152	221	231	220	231	160	173	277	279	178	194	135	135
TNSW	H-R767	159	159	103	109	150	152	223	223	224	229	156	171	279	281	175	178	133	135
TNSW	H-R769	159	159	109	117	152	152	195	219	227	227	153	160	279	279	175	190	133	133
TNSW	H-R773	159	159	103	107	150	152	223	239	224	229	156	158	277	281	175	194	133	135
TNSW	H-R775	0	0	103	103	152	152	195	195	220	227	156	0	279	281	176	0	133	149
TNSW	H-R783	159	159	105	124	152	152	213	213	220	229	158	173	279	281	175	182	133	149
TNSW	H-R787	159	159	107	119	150	152	213	225	224	224	0	173	277	281	175	182	133	133
TNSW	H-R789	159	159	113	124	150	152	213	0	220	224	156	173	281	281	175	182	133	133
TNSW	H-RA02	159	159	119	124	152	152	213	237	229	229	153	156	279	279	175	196	135	151
TNSW	H-RA05	159	175	105	122	152	152	213	237	229	229	156	177	279	281	175	175	133	133
TNSW	H-RA07	159	159	107	119	152	152	213	221	220	220	160	173	277	279	190	194	133	135
TNSW	H-RA10	159	159	107	124	152	152	227	231	218	224	158	160	279	285	175	176	135	135
TNSW	H-RA12	159	159	103	103	150	152	231	233	229	229	156	160	279	279	175	190	133	133
TNSW	H-RA14	159	159	103	103	152	152	0	0	220	220	171	173	277	281	175	178	133	133
TNSW	H-RA16	159	159	107	124	152	152	219	237	220	229	153	160	279	279	175	192	135	151
TNSW	H-RA17	159	159	115	124	152	152	231	233	224	231	153	160	279	279	175	178	133	135
TNSW	H-RA20	159	159	109	126	152	152	215	221	227	233	175	177	279	279	175	194	133	135
TNSW	H-RA22	159	159	103	107	152	152	213	213	214	220	160	171	279	279	175	175	133	133
TNSW	H-RA24	159	159	115	124	150	152	195	195	220	224	160	169	279	281	175	194	133	133

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNSW	H-RA26	159	159	103	107	150	152	237	239	218	220	158	173	277	279	176	194	135	135
TNSW	H-RA28	159	159	115	124	152	152	195	213	220	231	160	177	279	281	175	175	133	135
TNSW	H-RA30	161	161	107	107	152	152	195	195	214	229	160	160	279	279	176	190	133	135
TNSW	H-RA307	159	159	103	126	150	152	219	223	220	229	153	158	281	281	175	175	133	133
TNSW	H-RA309	159	159	109	115	150	152	0	0	0	0	160	160	0	0	0	0	129	133
TNSW	H-RA32	159	159	103	111	150	152	197	231	224	224	156	175	279	279	175	176	133	133
TNSW	H-RA35	159	159	103	124	150	152	227	237	220	224	169	169	279	281	186	194	133	135
TNSW	H-RA37	159	159	103	103	150	152	195	195	220	227	160	173	277	281	175	196	133	133
TNSW	H-RA39	159	159	103	124	152	152	0	0	220	227	158	160	279	281	190	196	133	133
TNSW	H-RA41	159	159	103	107	152	152	0	0	220	229	160	162	279	279	175	192	133	151
TNSW	H-RA43	159	159	103	119	152	152	195	195	227	229	160	173	279	281	182	196	133	133
TNSW	H-RA45	0	0	103	124	0	0	213	227	229	229	158	177	279	279	0	0	133	133
TNSW	H-RA47	159	159	0	0	152	152	213	213	222	231	160	177	279	279	175	175	133	133
TNSW	H-RA49	161	161	107	124	152	152	231	237	220	224	160	160	277	279	176	192	133	151
TNSW	H-RA51	159	159	107	107	152	152	231	237	0	0	158	160	0	0	175	0	135	151
TNSW	H-RA53	161	161	107	119	152	152	0	213	220	229	160	177	277	279	0	192	133	133
TNSW	H-RA601	159	159	105	119	152	152	213	213	229	229	173	177	279	279	175	182	133	149
TNSW	H-RA603	159	159	109	119	150	152	231	233	220	229	166	175	279	281	175	194	135	135
TNSW	H-RA605	159	159	115	128	152	152	223	223	227	229	175	175	279	281	175	175	133	155
TNSW	H-RA607	159	159	109	128	152	152	195	195	218	229	160	177	277	279	175	175	133	133
TNSW	H-RA610	159	159	105	115	152	152	223	223	216	0	160	175	279	279	175	175	133	137
TNSW	H-RA801	159	159	103	103	152	152	227	237	214	224	160	173	279	281	175	175	133	133
TNSW	H-RA804	159	159	109	111	150	152	227	233	220	229	175	179	279	279	175	175	133	133

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNSW	H-RA806	159	159	103	124	152	152	225	225	220	222	153	173	279	279	175	175	133	135
TNSW	H-RA808	157	159	105	107	150	152	195	195	0	0	160	173	279	281	175	175	133	133
TNSW	H-RA810	159	159	107	115	150	152	221	237	220	220	160	160	277	279	182	194	133	133
TNSW	H-RA820	159	159	107	124	150	152	227	227	220	220	156	173	281	281	175	176	133	133
TNSW	H-RA822	159	159	105	124	152	152	195	195	224	229	158	0	279	281	175	175	133	133
TNSW	H-RA824	159	159	103	119	152	152	0	0	218	222	166	173	279	281	194	196	133	133
TNSW	H-RA827	159	159	105	115	150	152	195	195	224	229	160	173	279	281	175	190	133	133
TNSW	H-RA830	159	159	107	107	150	152	0	0	222	224	160	162	279	281	175	182	133	133
TNSW	H-RA834	159	159	103	128	150	152	213	213	220	229	153	160	281	281	175	175	133	133
TNSW	H-RA836	159	159	103	103	152	152	227	245	220	220	153	156	279	281	175	175	133	135
TNSW	H-RA838	159	159	107	113	150	152	179	179	224	227	162	173	277	281	175	194	133	133
TNSW	H-RA842	159	159	103	107	150	150	231	245	224	224	173	0	277	281	178	194	133	133
TNSW	H-RA846	159	159	107	119	150	152	195	231	220	224	173	173	279	281	178	178	133	135
TNSW	H-RA870	159	159	113	119	152	152	225	237	218	224	158	162	279	281	175	190	133	133
TNSW	H-RUM309	159	159	103	119	152	152	223	237	224	229	173	179	279	279	175	175	133	135
TNSW	H-RUM325	159	159	103	107	150	152	195	195	220	224	158	173	0	0	175	194	133	135
TNSW	H-RUM709	159	159	107	107	152	152	235	237	218	229	158	160	277	279	175	194	133	133
TNSW	H-RUM753	159	159	107	109	150	152	213	223	229	229	156	156	279	281	175	178	135	135
TNSW	H-RUM755	159	159	103	124	152	152	213	213	220	227	160	160	279	281	175	176	133	133
TNSW	MC-R2441	159	159	103	107	150	150	223	243	214	224	168	173	281	281	175	188	133	133
TNSW	MC-R526	159	159	103	105	150	152	227	245	220	224	156	171	277	279	178	190	133	149
TNSW	MC-R904	159	159	111	115	150	152	215	241	220	224	153	158	279	279	194	194	133	133
TNSW	MC-R930	159	159	109	122	152	152	213	233	224	224	160	162	279	279	175	176	133	133

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNSW	MC-R935	159	159	124	124	150	152	227	237	220	224	153	158	279	283	175	194	133	133
TNSW	MC-R942	159	159	107	115	152	152	223	241	220	224	153	166	279	279	175	194	133	133
TNSW	MC-R973	159	159	119	122	152	152	219	229	214	229	153	160	279	279	175	176	133	133
TNSW	MC-R978	159	159	111	115	150	152	201	221	229	233	153	175	279	281	175	190	133	133
TNSW	MC-RA180	159	159	103	103	152	152	225	227	218	222	160	160	279	279	175	182	133	155
TNSW	MC-RA190	159	159	107	115	150	152	237	241	0	229	153	0	279	279	175	175	133	133
TNSW	MC-RA209	159	159	111	122	150	152	215	237	224	224	158	173	279	279	175	194	133	133
TNSW	MC-RA304	159	159	109	111	152	152	0	0	216	231	160	173	279	279	175	190	133	133
TNSW	MC-RA876	159	159	103	119	150	152	0	0	0	0	0	0	0	0	176	192	133	133
TNSW	MC-RUM841	159	159	103	103	150	152	213	213	214	224	160	173	279	279	175	176	133	133
TNSW	MC-RUM843	159	159	103	119	150	152	237	239	214	220	160	0	279	279	175	188	133	135
TNSW	MC-RUM851	159	159	103	109	152	152	225	225	220	222	153	160	279	279	175	194	133	135
TNSW	MC-RUM860	159	159	115	124	150	152	195	195	220	231	162	177	279	279	175	178	133	133
TNSW	MC-RUM901	159	175	0	115	0	0	221	237	220	229	0	0	279	281	175	188	133	135
TNSW	MC-RUM909	159	159	107	119	150	152	221	237	222	224	166	169	279	281	175	188	133	133
TNSW	MC-RUM912	159	159	103	105	152	152	195	195	216	224	160	179	279	281	175	182	133	133
TNSW	MC-RUM943	159	159	103	115	150	152	195	195	216	229	153	179	279	279	175	175	133	133
TNSW	MC-RUM945	159	159	115	119	152	152	221	223	220	222	166	166	279	281	188	194	133	135
TNSW	MC-RUM949	159	159	113	115	152	152	223	229	224	224	158	177	279	279	175	175	133	133
TNSW	MC-RUM951	159	159	117	119	150	152	225	231	220	220	156	156	277	279	175	175	135	147
TNSW	MC-RUM954	159	159	105	122	152	152	195	195	218	220	162	162	281	281	175	192	133	133
TNSW	MC-RUM960	159	159	115	115	150	152	223	241	220	229	153	166	279	279	175	194	133	135
TNSW	MC-RUM970	159	159	105	115	150	152	239	241	216	229	151	160	279	279	175	175	133	133

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNSW	MC-RUM980	159	159	103	113	150	152	219	237	227	229	153	153	277	281	175	176	133	133
TNSW	M-R1999	159	159	105	115	152	152	221	241	214	231	158	175	279	279	175	194	133	151
TNSW	M-R5782	159	159	109	119	150	150	229	231	224	229	153	160	279	279	176	190	135	135
TNSW	M-R606	159	159	105	117	150	152	217	231	229	229	160	177	0	0	176	178	133	133
TNSW	M-R609	161	161	103	103	150	152	0	0	220	227	149	160	279	279	176	190	133	149
TNSW	M-R610	159	159	111	115	152	152	233	235	224	227	158	177	279	279	178	194	155	155
TNSW	M-R6101	159	159	115	117	150	150	195	0	222	224	162	162	277	281	175	175	133	133
TNSW	M-R6103	159	159	115	122	0	152	0	0	0	0	158	0	279	279	175	0	133	0
TNSW	M-R6112	159	159	119	124	150	150	0	0	216	224	160	160	279	279	190	190	135	135
TNSW	M-R6117	159	159	109	122	152	157	213	229	218	227	160	162	279	281	175	194	133	133
TNSW	M-R6122_1	159	159	109	117	150	152	223	223	218	229	162	177	279	279	175	188	151	151
TNSW	M-R6123	159	159	103	105	152	152	199	229	214	231	160	162	277	279	175	196	133	133
TNSW	M-R6125	159	159	109	113	152	152	197	197	224	227	160	162	279	279	175	175	133	133
TNSW	M-R6126	159	159	105	117	152	152	199	229	214	231	160	160	277	279	190	194	133	151
TNSW	M-R6132	159	159	103	117	150	152	215	215	216	216	160	169	279	279	175	175	133	133
TNSW	M-R6133	159	159	109	115	150	150	225	227	220	231	156	160	277	281	190	192	133	133
TNSW	M-R6142	159	179	105	117	150	152	217	231	229	229	160	175	279	279	178	192	133	135
TNSW	M-R6145	159	159	070	076	152	152	0	0	220	227	156	158	277	279	175	188	133	133
TNSW	M-R6148	159	159	105	117	152	152	199	239	214	227	160	160	279	281	190	194	133	133
TNSW	M-R616	159	159	103	109	152	152	0	0	222	224	155	177	281	281	175	175	133	151
TNSW	M-R6174	159	159	113	122	152	152	221	223	220	227	162	177	279	279	176	178	147	155
TNSW	M-R618	159	159	109	109	152	152	219	219	224	227	149	160	277	281	175	175	133	135
TNSW	M-R619	159	159	109	111	150	152	235	235	218	224	160	173	279	279	175	175	133	151

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNSW	M-R622	159	159	113	122	152	157	223	223	227	227	160	162	279	281	176	178	133	133
TNSW	M-R624_673	159	159	113	122	152	152	223	223	220	227	162	177	279	279	176	178	0	0
TNSW	M-R625	159	159	103	105	152	152	197	197	227	227	153	160	279	279	175	176	133	133
TNSW	M-R626	159	179	0	0	152	152	221	229	227	229	158	177	279	281	175	190	133	135
TNSW	M-R6308	159	159	103	109	152	152	225	235	220	224	151	160	281	281	186	196	133	133
TNSW	M-R6312	159	159	109	117	152	152	0	0	214	220	160	160	281	281	175	190	133	133
TNSW	M-R6313	159	159	103	124	150	152	197	197	214	220	153	175	279	279	175	194	133	133
TNSW	M-R6314	159	159	107	115	152	152	197	215	220	231	158	173	281	281	175	194	133	133
TNSW	M-R6315	159	159	107	109	152	152	225	229	218	222	0	177	279	279	175	192	133	151
TNSW	M-R6316	159	159	107	117	152	152	0	0	214	216	160	160	279	279	175	194	133	133
TNSW	M-R6318	159	159	119	119	150	152	229	231	224	227	153	160	279	279	176	176	133	135
TNSW	M-R6319	159	159	103	107	152	152	197	197	224	229	160	173	279	281	176	194	133	135
TNSW	M-R6324	159	159	109	113	152	157	219	219	216	0	156	173	279	281	175	175	133	135
TNSW	M-R6330	159	159	113	115	152	152	221	223	224	231	156	175	281	281	175	175	133	135
TNSW	M-R6333	159	159	103	119	152	152	0	0	214	227	160	177	279	279	176	194	133	133
TNSW	M-R6335	159	159	111	113	152	152	0	0	224	227	160	177	279	279	175	176	133	147
TNSW	M-R6337	159	159	107	115	152	152	221	221	214	216	158	160	279	279	175	175	133	133
TNSW	M-R6342	159	159	103	117	150	152	217	223	214	220	162	177	279	279	176	178	133	135
TNSW	M-R6344	159	159	115	117	152	152	227	229	214	227	153	160	279	279	175	194	133	133
TNSW	M-R6346	159	159	119	124	152	152	0	0	224	227	162	175	279	279	175	190	133	133
TNSW	M-R6348	159	159	105	122	150	152	0	0	224	229	160	166	277	281	175	175	133	0
TNSW	M-R6349	0	0	105	109	152	157	0	0	214	218	160	162	0	0	190	194	133	133
TNSW	M-R652	159	0	119	119	152	152	223	237	214	233	153	173	279	279	175	192	133	133



TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNSW	M-R656	159	159	103	117	152	152	237	239	214	224	160	177	279	279	175	194	133	133
TNSW	M-R659	159	159	109	115	152	152	219	235	227	229	160	160	279	281	175	175	133	133
TNSW	M-R664	159	159	109	109	150	152	221	227	224	227	160	175	277	279	175	176	133	133
TNSW	M-R669	159	159	105	122	152	152	199	223	220	227	160	177	279	279	176	196	133	147
TNSW	M-R673	159	159	105	107	150	152	0	0	224	231	160	160	0	0	175	194	133	133
TNSW	M-R675	159	159	105	117	152	152	225	239	214	231	160	160	277	279	194	194	133	151
TNSW	M-R681	159	159	103	103	150	152	231	235	224	229	158	160	279	279	175	175	133	135
TNSW	M-R687	159	159	105	124	150	152	219	225	214	222	160	177	279	279	175	186	133	133
TNSW	M-R688	159	159	086	109	152	152	211	235	220	220	158	162	279	279	175	194	133	133
TNSW	M-R689	159	159	103	115	150	150	227	227	220	229	160	173	277	279	175	175	135	0
TNSW	M-R694	159	159	113	115	150	152	223	223	224	231	156	175	281	281	175	175	133	135
TNSW	M-R696	159	159	070	086	0	0	0	0	227	229	162	162	279	279	175	190	133	135
TNSW	M-R697	159	159	103	117	152	152	225	225	224	231	160	177	277	279	175	194	133	151
TNSW	M-R698	159	159	070	086	152	152	221	221	220	224	158	160	279	279	175	194	133	151
TNSW	M-R700	159	159	103	117	150	152	195	225	218	218	160	162	279	279	175	175	133	151
TNSW	M-R710	159	159	107	115	150	152	193	193	214	216	158	160	279	279	175	190	135	151
TNSW	M-R716	159	159	103	122	152	152	221	221	218	229	160	160	277	281	175	175	133	135
TNSW	M-R717	159	159	103	117	152	152	221	229	214	220	158	162	279	279	186	192	133	133
TNSW	M-R721	159	159	105	115	152	157	219	219	214	222	153	158	279	279	175	175	133	133
TNSW	M-RA102	159	159	109	115	150	152	197	219	224	227	160	175	279	281	175	175	133	133
TNSW	M-RA104	159	159	109	111	150	152	221	221	224	227	158	160	279	281	175	192	133	135
TNSW	M-RA106	159	159	117	119	152	152	227	229	214	227	153	160	279	279	175	194	133	133
TNSW	M-RA108	159	159	115	119	152	152	227	229	220	227	153	160	279	279	176	178	133	133

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNSW	M-RA110	159	159	103	105	150	152	219	235	220	227	160	177	279	279	175	175	133	133
TNSW	M-RA116	0	0	113	115	150	152	215	229	224	224	160	162	279	281	175	175	133	133
TNSW	M-RA118	159	159	109	115	150	152	227	229	218	220	162	175	279	281	175	175	133	133
TNSW	M-RA120	159	159	105	119	152	152	229	239	224	227	160	175	281	281	175	196	133	135
TNSW	M-RA122	159	159	103	105	152	152	225	225	224	224	153	160	279	279	175	175	133	133
TNSW	M-RA124	161	161	113	115	152	152	235	235	224	229	160	162	281	281	176	176	133	133
TNSW	M-RA126	159	159	105	117	152	152	221	239	220	224	158	160	279	279	175	194	133	151
TNSW	M-RA128	159	159	103	109	150	152	215	235	224	227	153	160	279	281	175	175	133	135
TNSW	M-RA131	159	159	103	105	152	152	197	221	214	214	158	160	279	279	175	194	133	151
TNSW	M-RA133	159	159	105	119	150	152	187	223	214	227	158	160	277	279	190	190	133	133
TNSW	M-RA135	159	159	105	107	150	152	223	235	214	224	153	156	279	283	175	186	133	135
TNSW	M-RA137	159	159	109	122	152	152	223	233	224	227	153	158	279	279	175	196	133	133
TNSW	M-RA139	159	159	103	107	150	152	231	233	218	224	160	173	277	281	175	175	133	133
TNSW	M-RA140	159	159	103	122	150	152	197	197	227	227	162	166	279	279	175	194	133	133
TNSW	M-RA142	159	179	122	122	152	152	227	229	214	229	160	160	0	0	175	175	133	133
TNSW	M-RA146	159	159	117	119	152	152	219	243	220	227	158	158	279	279	175	194	133	133
TNSW	M-RA148	159	159	105	119	152	152	199	235	214	227	153	160	279	279	175	175	133	151
TNSW	M-RA149	159	159	103	111	152	152	223	235	216	218	160	171	279	279	175	192	133	133
TNSW	M-RA277	161	161	105	124	157	159	199	229	227	227	0	0	0	0	0	0	0	0
TNSW	M-RA278	159	159	103	122	152	152	231	237	214	222	162	175	279	279	190	194	133	133
TNSW	M-RA280	159	159	103	111	150	152	223	223	224	224	160	162	279	279	175	175	133	133
TNSW	M-RA281	159	159	086	101	0	0	223	225	220	220	160	162	279	279	175	178	133	0
TNSW	M-RA282	159	159	111	115	152	152	235	235	227	227	158	177	279	279	178	194	155	155

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNSW	M-RA283	159	159	107	107	152	152	192	221	214	216	162	175	279	279	175	190	133	133
TNSW	M-RA285	159	159	103	113	152	152	0	0	220	229	162	162	279	279	175	178	133	147
TNSW	M-RA290	159	159	113	113	152	152	197	197	224	227	162	177	279	279	175	178	133	155
TNSW	M-RA293	159	159	070	086	150	152	225	235	220	224	149	160	281	281	186	196	133	133
TNSW	M-RA322	159	159	103	109	152	152	225	233	220	227	177	177	277	279	175	175	133	133
TNSW	M-RA324	159	159	115	119	152	152	197	229	227	227	156	160	279	279	176	178	133	133
TNSW	M-RA377	0	0	0	0	152	152	239	0	218	229	0	0	279	279	175	192	133	133
TNSW	M-RA380	0	0	103	117	150	152	213	231	229	229	153	162	279	279	175	175	133	133
TNSW	M-RA381	159	159	0	0	150	152	221	223	224	224	160	177	279	281	175	175	133	133
TNSW	M-RA438	159	159	103	115	152	152	197	225	220	224	156	160	279	279	175	188	133	133
TNSW	M-RA447	159	159	111	115	150	152	0	0	214	216	160	162	279	279	175	196	133	135
TNSW	M-RA457	159	159	105	117	152	152	219	219	214	220	158	160	279	279	175	176	133	133
TNSW	M-RA478	159	159	122	122	152	152	233	235	214	229	162	162	277	279	175	176	133	147
TNSW	M-RA500	159	159	103	119	150	152	197	197	214	224	173	177	279	279	176	194	133	133
TNSW	M-RA501	159	159	103	109	150	150	219	223	214	224	160	160	279	281	175	175	133	135
TNSW	M-RA503	159	159	117	124	152	152	0	0	229	229	160	177	279	279	175	175	133	133
TNSW	M-RA506	159	159	105	109	152	152	213	241	214	224	160	175	279	279	175	175	133	133
TNSW	M-RA508	159	159	103	119	152	152	213	239	224	224	160	177	279	281	175	175	133	133
TNSW	M-RA510	159	159	103	113	152	152	223	229	214	227	160	177	279	279	175	192	133	133
TNSW	M-RA512	159	159	111	115	152	152	197	197	218	218	166	171	279	281	175	175	129	133
TNSW	M-RA514	159	159	105	113	152	152	0	0	227	231	160	162	279	279	178	194	133	155
TNSW	M-RA516	159	159	111	115	152	152	233	235	227	227	158	177	279	279	175	178	133	155
TNSW	M-RA518	159	159	111	117	152	152	0	0	218	227	156	173	277	279	175	188	133	133

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNSW	M-RA521	159	159	109	115	150	152	215	221	229	229	158	160	281	281	175	175	133	133
TNSW	M-RA522	159	159	103	109	150	152	197	197	214	229	162	177	279	283	175	188	133	135
TNSW	M-RA524	159	159	103	103	150	152	223	223	218	218	160	177	279	279	175	178	133	133
TNSW	M-RA526	159	159	107	109	150	152	197	227	220	224	160	177	279	281	190	192	133	133
TNSW	M-RA529	159	159	103	111	152	152	225	233	220	224	156	158	279	281	175	175	133	147
TNSW	M-RA530	159	159	109	117	152	152	229	239	220	227	160	160	279	281	175	190	133	133
TNSW	M-RA540	161	161	105	109	0	0	223	229	220	224	162	175	279	281	176	176	133	155
TNSW	M-RA543	159	159	107	107	157	157	229	229	229	231	158	160	277	281	175	175	133	133
TNSW	M-RA551	159	159	105	124	150	152	0	0	214	229	162	177	279	281	175	190	133	133
TNSW	M-RA553	159	159	103	103	150	152	213	213	229	229	0	162	277	279	175	175	133	0
TNSW	M-RA555	159	159	103	119	152	152	229	229	224	229	160	175	279	281	175	175	133	135
TNSW	M-RA557	159	159	111	119	152	152	229	229	224	224	162	175	279	281	175	175	133	135
TNSW	M-RA561	159	159	103	117	150	152	223	223	214	214	160	160	279	279	176	178	133	135
TNSW	M-RA564	159	159	103	111	152	152	227	233	227	231	153	153	279	281	175	175	133	135
TNSW	M-RA565	159	159	0	0	152	152	213	235	214	227	156	160	277	281	0	0	133	133
TNSW	M-RA567	159	159	103	119	150	152	215	225	218	220	160	162	279	281	178	194	133	137
TNSW	M-RA573	159	159	103	105	150	152	219	225	214	224	162	162	279	279	0	0	133	133
TNSW	M-RA574	159	159	0	0	150	152	227	227	224	224	162	177	277	279	175	176	133	133
TNSW	M-RA717	159	159	0	0	150	152	215	241	214	216	160	160	277	279	175	176	133	135
TNSW	M-RA731	159	159	105	122	152	152	223	223	220	220	160	162	279	279	175	178	133	155
TNSW	M-RA733	159	179	117	122	152	152	0	0	214	227	160	177	279	279	175	176	133	147
TNSW	M-RA740	159	159	103	111	152	152	229	229	224	229	162	162	279	279	175	175	133	133
TNSW	M-RUM612	159	159	105	117	152	152	199	199	214	227	160	160	279	281	190	196	133	133

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNSW	M-RZ051	159	159	105	109	150	152	221	235	229	231	160	177	277	279	175	186	133	133
TNSW	M-RZ071	159	159	109	109	150	152	229	233	220	231	156	175	279	281	175	175	133	133
TNSW	M-RZ072	159	159	107	122	152	152	213	213	216	227	160	171	279	279	175	175	133	133
TNSW	M-RZ073	159	159	109	115	150	152	195	195	222	227	162	177	277	279	175	175	133	133
TNSW	M-RZ075	159	159	111	117	150	157	213	213	216	224	162	175	279	279	175	176	133	133
TNSW	M-RZ102	159	159	103	124	152	152	223	233	216	231	160	166	279	281	175	190	133	135
TNSW	M-RZ105	159	159	103	103	150	152	197	197	212	214	160	160	279	279	175	178	133	135
TNSW	M-RZ106	159	159	105	117	150	152	233	237	224	229	153	160	279	281	175	194	133	135
TNSW	M-RZ108	159	159	113	124	150	152	213	213	218	224	162	175	279	281	175	186	133	133
TNSW	M-RZ110	159	159	105	117	152	152	195	221	214	214	177	177	279	279	175	186	133	133
TNSW	M-RZ112	159	159	103	105	150	152	211	219	214	224	158	160	279	279	175	194	133	135
TNSW	M-RZ115	159	159	105	122	152	152	219	219	220	227	166	177	279	279	175	176	133	147
TNSW	M-RZ119	159	159	103	124	152	152	225	225	224	224	160	160	279	281	175	188	133	133
TNSW	M-RZ120	159	159	103	117	150	152	221	223	224	224	160	177	279	279	175	0	133	135
TNSW	M-RZ124	159	159	103	109	150	152	219	219	214	227	160	177	279	279	175	194	133	135
TNSW	P-R204	159	159	115	119	150	152	225	243	222	233	175	177	279	281	175	175	133	133
TNSW	P-R223	159	159	105	105	152	152	235	237	229	229	151	173	279	281	175	182	133	135
TNSW	P-R228	159	159	115	117	0	152	0	0	214	0	153	162	0	0	0	0	135	135
TNSW	P-R247	159	159	103	124	150	152	215	227	224	224	175	177	279	279	175	176	129	133
TNSW	P-R249	159	159	103	115	152	152	0	0	229	231	158	160	279	279	176	176	133	133
TNSW	P-R252	159	159	115	124	150	152	225	237	214	220	153	162	277	279	175	182	135	135
TNSW	P-R256	159	159	103	115	152	152	219	221	220	229	162	173	279	281	175	175	133	133
TNSW	P-R315	159	159	124	124	150	157	219	219	0	0	162	173	0	0	0	0	135	149

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TNSW	P-R511	159	159	105	122	152	152	231	233	214	216	168	0	277	279	175	196	133	133
TNSW	P-R574	159	159	103	119	150	152	227	227	220	220	160	166	279	281	176	176	133	135
TNSW	P-RA386	159	159	0	0	150	152	235	237	220	229	160	160	277	281	175	192	133	135
TNSW	P-RA387	159	159	109	115	150	152	217	221	220	224	173	175	279	281	175	175	133	133
TNSW	P-RA390	159	159	107	113	152	152	217	231	216	227	153	173	279	279	175	175	133	133
TNSW	P-RA393	159	159	103	115	152	152	247	249	229	231	160	166	281	281	175	194	133	133
TNSW	P-RA396	159	159	109	111	152	152	213	213	229	235	173	175	281	281	175	175	133	135
TNSW	P-RA397	159	159	0	0	150	152	0	0	218	227	160	162	0	0	175	176	133	135
TNSW	P-RA400	159	159	103	109	150	152	221	237	214	224	158	177	277	279	176	182	133	149
TNSW	P-RA614	159	159	103	124	150	152	197	197	220	229	160	160	279	279	175	175	133	133
TNSW	P-RA616	159	159	111	119	152	152	225	225	222	231	166	166	281	281	175	194	133	135
TNSW	P-RA621	159	159	103	109	152	152	219	219	216	233	160	160	277	279	175	175	133	135
TNSW	P-RA623	159	159	111	124	152	152	235	237	220	229	160	177	279	279	175	194	133	133
TNSW	P-RA625	159	159	103	124	152	152	213	213	216	229	<u>0</u>	<u>0</u>	277	279	175	194	133	135
TNSW	P-RUM211	159	159	103	107	152	152	213	219	220	222	160	162	279	281	175	175	133	135
TNSW	P-RUM217	159	159	107	115	152	152	219	219	224	227	160	180	0	0	175	175	133	133
TNSW	P-RUM221	159	159	107	115	0	0	207	229	224	227	153	160	0	0	182	194	133	133
TNSW	P-RUM231	159	159	103	119	150	152	219	233	220	224	171	175	279	281	175	175	133	133
TNSW	P-RUM235	159	0	122	124	150	150	195	195	0	0	<u>0</u>	<u>0</u>	279	279	194	194	133	135
TNSW	P-RUM266	159	159	109	115	152	152	231	233	<u>220</u>	<u>0</u>	153	173	281	281	175	175	133	149
TNSW	P-RUM274	159	159	119	119	152	152	213	237	222	224	156	156	279	281	194	194	133	133
TX	TX-1395	161	161	109	122	150	152	0	0	210	227	155	166	0	0	176	0	133	133
TX	TX-1397	159	159	103	119	152	157	171	171	214	222	166	171	279	279	175	176	133	133

TABLE 1.—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
TX	TX-1398	159	159	103	109	152	157	171	171	214	222	166	171	279	281	175	176	133	133
TX	TX-1400	159	159	107	113	150	152	0	0	0	0	153	160	0	0	176	192	133	133
TX	TX-1401	159	159	119	126	150	150	225	227	222	224	158	175	279	279	175	175	135	135
TX	TX-1404	161	161	103	107	150	150	223	225	227	227	160	173	279	279	175	188	133	133
TX	TX-1405	161	161	109	119	152	157	215	235	224	229	160	171	279	279	176	190	133	133
TX	TX-1406	159	159	103	119	157	157	221	223	214	224	160	175	279	279	175	196	133	133
TX	TX-1407	159	159	122	124	150	150	223	225	227	227	160	173	279	279	175	175	133	133
TX	TX-1408	161	161	103	107	152	155	205	237	214	227	160	166	279	279	178	184	133	155
TX	TX-1409	159	159	103	107	150	150	223	225	224	227	160	162	277	279	175	188	133	133
TX	TX-1410	161	161	105	115	152	152	225	235	224	229	160	171	279	279	175	190	133	133
TX	TX-1411	159	159	103	119	150	150	0	0	224	227	166	180	279	281	175	175	133	133
WI	WI-1063	159	159	107	122	152	152	231	231	224	227	153	173	277	279	175	175	133	133
WI	WI-1064	159	159	105	109	152	157	0	0	220	222	151	153	279	283	176	176	133	133
WI	WI-1065	159	159	105	107	152	157	217	217	204	227	151	151	279	281	175	176	133	133
WI	WI-1066	159	159	105	109	152	155	229	237	204	218	156	160	277	279	175	176	133	137
WI	WI-1068	159	159	103	113	152	155	205	217	214	227	171	171	279	283	175	175	133	153
WI	WI-1069	159	159	105	107	150	152	197	197	227	227	153	160	281	281	175	196	133	133
WI	WI-1070	159	159	115	124	152	152	179	201	222	227	151	180	0	0	175	194	133	135
WI	WI-1071	159	159	107	124	152	152	215	231	222	229	160	160	277	279	175	176	133	133
WI	WI-1072	159	159	103	115	152	152	215	231	218	229	156	162	279	279	175	176	133	135
WI	WI-1073	159	159	105	107	150	152	221	225	218	227	156	173	279	281	175	175	133	135
WI	WI-1075	159	159	117	124	152	152	0	0	222	227	156	160	277	279	175	194	133	133
WI	WI-1076	159	159	105	117	152	152	227	233	222	227	156	184	277	279	175	175	133	133

**TABLE 1.**—Continued.

Site	ID	G10B		G10C		G10X		PFL4		PFL9		PFL11		PL35		PL40		PL61	
WI	WI-1077	159	159	109	109	150	152	0	0	227	227	156	156	0	0	175	196	133	135
WI	WI-1078	159	159	111	115	152	152	215	231	222	227	156	173	0	0	175	176	133	135
WI	WI-1080	159	159	105	111	152	152	227	229	214	222	160	177	277	281	175	196	133	135