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Ecology of the Eastern Cottonmouth (*Agkistrodon p. piscivorus*) at Back Bay National Wildlife Refuge: A Comparative Study of Natural and Anthropogenic Marsh Habitats

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ECOLOGY OF THE EASTERN COTTONMOUTH (*AGKISTRODON P. PISCIVORUS*)
AT BACK BAY NATIONAL WILDLIFE REFUGE: A COMPARATIVE STUDY OF
NATURAL AND ANTHROPOGENIC MARSH HABITATS

by

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ABSTRACT

ECOLOGY OF THE EASTERN COTTONMOUTH (*AGKISTRODON P. PISCIVORUS*) AT BACK BAY NATIONAL WILDLIFE REFUGE: A COMPARATIVE STUDY OF NATURAL AND ANTHROPOGENIC MARSH HABITATS.

Chad L. Cross
Old Dominion University, 1998
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Mark-recapture sampling and radiotelemetry were used to investigate populations of the eastern cottonmouth, *Agkistrodon p. piscivorus*, in both natural and anthropogenic marsh habitats at Back Bay National Wildlife Refuge (BBNWR), Virginia Beach, Virginia from autumn 1995 to late spring 1998. Mark-recapture subjects were captured, marked by ventral scale-clipping, and released back into the population. A modified Schnabel Census estimator was used to estimate population sizes and corresponding densities in both marsh systems based on a total of 244 captures of 222 individuals. Most snakes were found > 0.05 m from water, but it was apparent that proximity to water played a major role in the distribution of these snakes. Most snakes were found with the body extended and in direct sunlight regardless of temperature; live vegetation served as the primary cover object for these snakes. The majority of captures were male snakes, and few gravid females were captured in either marsh in either year. Many snakes fled before capture. Snakes fled in the direction opposite the investigator no matter which medium (land or water) they occupied at the time. Aggressive behaviors were rare. Radiotelemetry subjects were captured, removed to the laboratory for radiotransmitter implantation, and subsequently released at the initial capture location. Snakes were tracked from 83-208 days, and between 54 and 101 observations were made for each subject. Snakes in the anthropogenic marsh moved greater overall distances than did snakes in the natural marsh. Discriminant Function Analysis based on comparisons of use and non-use sites and

Polytomous Logistic Regression, based on use-intensity classification of sites used by radiotelemetry subjects both suggested that the most important habitat variables for determining sites used by cottonmouths in both marshes were: distance to water, distance to overstory trees, leaf litter cover, and vegetation cover. Gut analyses suggested that frogs (*Rana* spp.) and sunfishes (*Lepomis* spp.) were the primary prey sources. Snakes hibernated both singly and together. The greatest single concern for future populations of cottonmouths at BBNWR is likely the availability of adequate cover, particularly in terms of the conversion of areas containing hibernacula to management impoundments.

To John Leo Davis:
physicist, astronomer, outdoorsman,
friend, mentor, and teacher of sixth grade science.
You were right, John. Science is fun.

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TABLE OF CONTENTS

	Page
LIST OF TABLES.....	viii
LIST OF FIGURES.....	xvi
INTRODUCTION.....	1
SYSTEMATICS AND ECOLOGY OF <i>AGKISTRODON PISCIVORUS</i>	2
HABITAT.....	5
HABITAT USE AND SELECTION BY SNAKES.....	6
MODELING HABITAT USE.....	7
POPULATION ESTIMATION.....	8
ESTIMATION OF SNAKE ABUNDANCE.....	9
TROPHIC ECOLOGY AND BEHAVIOR.....	10
ACTIVITY RANGES AND MOVEMENTS.....	12
HIBERNATION.....	15
MATERIALS AND METHODS.....	17
STUDY SITE.....	17
CAPTURE AND MEASUREMENTS.....	20
COLLECTION AND ANALYSIS OF DATA ON COTTONMOUTHS.....	21
HABITAT ANALYSIS.....	25
ESTIMATION OF POPULATION SIZE.....	34
TROPHIC ECOLOGY AND BEHAVIOR.....	38
RADIOTELEMETRY.....	39
MANAGEMENT OF COTTONMOUTHS.....	42
RESULTS.....	43
ECOLOGICAL ANALYSES.....	43
HABITAT ANALYSES.....	67
POPULATION ESTIMATION.....	85
FORAGING AND FEEDING ECOLOGY.....	89
RADIOTELEMETRY.....	92
VISITOR AND HUNTER REPORTS.....	111

	Page
DISCUSSION.....	119
ECOLOGICAL ANALYSIS.....	119
HABITAT ANALYSIS.....	122
POPULATION ESTIMATION.....	126
FORAGING AND FEEDING ECOLOGY.....	127
RADIOTELEMETRY.....	128
SIGHTINGS BY VISITORS AND HUNTERS.....	132
MANAGEMENT STRATAGIES.....	132
FINDINGS AND INTERPRETATIONS.....	136
LITERATURE CITED.....	140
APPENDICES	
PLANT LIST FOR BACK BAY NATIONAL WILDLIFE REFUGE.....	156
FIELD COLLECTION DATA SHEET.....	163
VITA.....	164

LIST OF TABLES

TABLE	Page
1. Description of variables assessed during captures and relocations of cottonmouths at Back Bay National Wildlife Refuge.....	22
2. Habitat variables measured at random sites, capture sites, and sites occupied by radio-tracked cottonmouths at Back Bay National Wildlife Refuge.....	26
3. Categories of random and <i>Agkistrodon p. piscivorus</i> sites used in habitat modelling comparisons. See text for explanation of sample sizes and description of sampling protocol for each category.....	28
4. Morphological measurements used in statistical comparisons for cottonmouths at Back Bay National Wildlife Refuge. Snout-vent length (SVL) is given, as are measurements/SVL ratios. Measurements are presented as \bar{x} (n , SE).....	44
5. Results of MANOVA testing for differences in morphological characteristics of snake populations between natural and anthropogenic marsh systems at Back Bay National Wildlife Refuge. Morphological characters were divided by snout-vent length prior to analysis (see text). Wilks' Lambda for overall area effect is given.....	45
6. Results of MANOVA testing for differences in morphological characteristics of snake populations between sexes at Back Bay National Wildlife Refuge. Natural and anthropogenic populations were pooled prior to analysis since no area effect was found (see text). Morphological characters were divided by snout-vent length prior to analysis (see text). Wilks' Lambda for overall area effect is given.....	46

TABLE

Page

7. Difference measurements of cottonmouths at Back Bay National Wildlife Refuge. Growth (in mm) for two females and six males (natural and anthropogenic marsh systems are presented together; see text) separated by one year between initial capture and recapture are shown. Additionally, field versus laboratory measurements are given for five radiotelemetry snakes. Measurements are presented as \bar{x} (n, SE).....	48
8. Location for cottonmouths at Back Bay National Wildlife Refuge. Capture locations for mark-recapture snakes (NM-AF) and resight locations for radiotelemetry snakes (AP-1-AP-5) were placed into three categories and compared using chi-square tests with Yates' continuity correction (Sokal And Rohlf, 1995). Appropriate alpha-levels and degrees of freedom (total chi-square: $\alpha = 0.05$, $df = 2$; partial chi-square $\alpha = 0.01$, $df = 1$) are described in the text. Asterisks indicate statistical significance.....	49
9. Cover object data for cottonmouths at Back Bay National Wildlife Refuge. Cover type for mark-recapture snakes (NM-AF) and resight locations for radiotelemetry snakes (AP-1-AP-5) were placed into three categories and compared using chi-square tests with Yates' continuity correction (Sokal and Rohlf, 1995). Appropriate alpha-levels and degrees of freedom (total chi-square: $\alpha = 0.05$, $df = 2$; partial chi-square $\alpha = 0.01$, $df = 1$) are described in the text. Asterisks indicate statistical significance.....	51
10. Sun exposure for cottonmouths at Back Bay National Wildlife Refuge. Capture locations for mark-recapture snakes (NM-AF) and resight locations for radiotelemetry snakes (AP-1-AP-5) were placed into three categories and compared using chi-square tests with Yates' continuity correction (Sokal and Rohlf, 1995). Appropriate alpha-levels and degrees of freedom (total chi-square: $\alpha = 0.05$, $df = 2$; partial chi-square	

TABLE

Page

$\alpha = 0.01$, $df = 1$) are described in the text. Asterisks indicate statistical significance.....	53
11. Activity for cottonmouths at Back Bay National Wildlife Refuge. Activity for mark-recapture snakes (NM-AF) and resight locations for radiotelemetry snakes (AP-1-AP-5) were placed into three categories and compared using chi-square tests with Yates' continuity correction (Sokal and Rohlf, 1995). Appropriate alpha-levels and degrees of freedom (total chi-square: $\alpha = 0.05$, $df = 2$; partial chi-square $\alpha = 0.01$, $df = 1$) are described in the text. Asterisks indicate statistical significance.....	60
12. Defensive movement for cottonmouths at back bay national wildlife refuge. Defensive movement for mark-recapture snakes (NM-AF) and resight locations for radiotelemetry snakes (AP-1-AP-5) were placed into three categories and compared using chi-square tests with Yates' continuity correction (Sokal and Rohlf, 1995). Appropriate alpha-levels and degrees of freedom (total chi-square: $\alpha = 0.05$, $df = 2$; partial chi-square $\alpha = 0.01$, $df = 1$) are described in the text. Asterisks indicate statistical significance.....	62
13. Defensive behavior for cottonmouths at Back Bay National Wildlife Refuge. Behavior data for mark-recapture snakes (NM-AF) and resight locations for radiotelemetry snakes (AP-1-AP-5) were placed into three categories and compared using chi-square tests with Yates' continuity correction (Sokal and Rohlf, 1995). Appropriate alpha-levels and degrees of freedom (total chi-square: $\alpha = 0.05$, $df = 2$; partial chi-square $\alpha = 0.01$, $df = 1$) are described in the text. Asterisks indicate statistical significance.....	64

TABLE	Page
14. Contingency table for 53 cottonmouths that escaped capture at Back Bay National Wildlife Refuge. Snakes from natural and anthropogenic marsh systems were pooled prior to analysis (see text). Data are presented according to the medium from which approach was made and to which medium the snake fled and subsequently evaded capture.....	66
15. Means and standard errors (given in parentheses) of habitat variables for each snake or random category. Habitat variables are given in Table 2. Snake and random categories are given in Table 3.....	68
16. Results of Tukey's Studentized Range (HSD) Test for distance to water (m). Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.....	69
17. Results of Tukey's Studentized Range (HSD) Test for diameter at breast height of overstory tree (cm). Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.....	71
18. Results of Tukey's Studentized Range (HSD) Test for distance to overstory tree (m). Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.....	72
19. Results of Tukey's Studentized Range (HSD) Test for diameter at breast height of understory tree (cm). Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.....	73
20. Results of Tukey's Studentized Range (HSD) Test for distance to understory tree (m). Comparisons significant	

TABLE	Page
at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.....	74
21. Results of Tukey's Studentized Range (HSD) Test for percent canopy closure. Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.....	76
22. Results of Tukey's Studentized Range (HSD) Test for percent leaf cover. Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.....	77
23. Results of Tukey's Studentized Range (HSD) Test for percent degree cover. Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.....	78
24. Results of Tukey's Studentized Range (HSD) Test for percent vegetation cover. Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.....	79
25. Results of Tukey's Studentized Range (HSD) Test for vegetation density (stems/m ²) measurements. Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.....	80
26. Results of Tukey's Studentized Range (HSD) Test for stem height of dominant vegetation (m). Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.....	82
27. Results of crossvalidation reclassification for the normal kernel density discriminant function analysis. Numbers shown are the percent of	

TABLE

Page

observations classified into a particular group (across the top of the table) from each category (down the left side). As an Example, 99% of the RN observations were classified into the RN category, and 1% of the RN observations were classified into the AF category, given the discriminant function. Categories are described in Table 3.....	83
28. Means and standard errors (in parentheses) for habitat variables for each use category in the polytomous logistic regression procedure. Habitat variables are given in Table 2. Category 1 = low-use grid cells, category 2 = medium-use grid cells, and category 3 = high-use grid cells. See text for description of technique and grid cell use selection criteria.....	86
29. Classification results for the polytomous logistic regression model. Numbers given are the percentage of observations classified into each category given the observed use-intensity level.....	87
30. Population size and density estimates given as estimate [and 95% confidence interval] for cottonmouths at Back Bay National Wildlife Refuge. See text for explantation of calculation methods. Areal density based on a sampling area of 1200 ha in the natural marsh and 1900 ha in the anthropogenic marsh. Linear density based on a transect length of 6340 m in the natural marsh and 9860 m in the anthropogenic marsh.....	88
31. Summary of food items collected from cottonmouths at Back Bay National Wildlife Refuge. Data are presented as total number of items per category, separated by marsh area and sex.....	90
32. Mean mass, volume, or dimensions and (standard errors) of items collected from cottonmouths at Back Bay National Wildlife Refuge. Food item data are in grams, liquid item data are in milliliters, and empty stomachs are given as a percentage of the total. Turtle mass was not	

TABLE

Page

determined; however, carapace dimensions were estimated in the field in millimeters.....	91
33. Movements of radiotracked snakes at Back Bay National Wildlife Refuge during the active season. Marsh location and sex are indicated by the following abbreviations: NM = male in natural marsh, AM = male in anthropogenic marsh, NF = female in natural marsh, and AF = female in anthropogenic marsh.....	99
34. Activity range areas and range lengths for radiotracked snakes at Back Bay National Wildlife Refuge. Marsh location and sex are indicated by the following abbreviations: NM = male in natural marsh, AM = male in anthropogenic marsh, NF = female in natural marsh, and AF = female in anthropogenic marsh.....	100
35. Minimum convex polygon activity areas of recaptured snakes at Back Bay National Wildlife Refuge. Male and female overall means (SE) are given.....	101
36. Mean body and environmental temperatures (C) for five radiotracked snakes at Back Bay National Wildlife Refuge during the active season. Marsh location and sex are indicated by the following abbreviations: NM = male in natural marsh, AM = male in anthropogenic marsh, NF = female in natural marsh, and AF = female in anthropogenic marsh. Data are presented as \bar{x} (n , SE).....	108
37. Mean body and environmental temperatures (C) for five radiotracked snakes at Back Bay National Wildlife Refuge during hibernation. Marsh location and sex are indicated by the following abbreviations: NM = male in natural marsh, AM = male in anthropogenic marsh, NF = female in natural marsh, and AF = female in anthropogenic marsh. Data are presented as \bar{x} (n , SE).....	109
38. Correlations for body temperature versus environmental temperatures during both the active season and hibernation for five radiotracked snakes at Back Bay National Wildlife Refuge. Marsh location and sex are indicated by the following abbreviations: NM = male in natural marsh,	

TABLE	Page
AM = male in anthropogenic marsh, NF = female in natural marsh, and AF = female in anthropogenic marsh data are presented as \bar{x} (n , SE).....	110

LIST OF FIGURES

FIGURE	Page
1. Area map for Back Bay National Wildlife Refuge showing both the natural marsh (area north of the Visitor Contact Station, Long Island, and Ragged Island) and the anthropogenic marsh (area south of the Visitor Contact Station). The Refuge is bordered by Little Island Park to the north and by False Cape State Park to the south. Refuge boundaries are shown by the dash-dot line.....	18
2. Location (As percentage of observations) for cottonmouths at Back Bay National Wildlife Refuge.....	50
3. Cover object (as percentage of observations) for cottonmouths at Back Bay National Wildlife Refuge.....	52
4. Sun exposure (as percentage of observations) for cottonmouths at Back Bay National Wildlife Refuge.....	54
5. Percentage of observations for sun exposure, activity, defensive behavior, and defensive movement plotted by temperature for mark-recapture male cottonmouths at Back Bay National Wildlife Refuge.....	56
6. Percentage of observations for sun exposure, activity, defensive behavior, and defensive movement plotted by temperature for mark-recapture female cottonmouths at Back Bay National Wildlife Refuge.....	57
7. Percentage of observations for sun exposure, activity, defensive behavior, and defensive movement plotted by temperature for radiotelemetered male cottonmouths at Back Bay National Wildlife Refuge.....	58

FIGURE	Page
8. Percentage of observations for sun exposure, activity, defensive behavior, and defensive movement plotted by temperature for radiotelemetered female cottonmouths at Back Bay National Wildlife Refuge.....	59
9. Activity (as percentage of observations) for cottonmouths at Back Bay National Wildlife Refuge.....	61
10. Defensive movement (as percentage of observations) for cottonmouths at Back Bay National Wildlife Refuge.....	63
11. Defensive behavior (as percentage of observations) for cottonmouths at Back Bay National Wildlife Refuge.....	65
12. Pooled Use-Intensity Categories for five radiotelemetered cottonmouths at Back Bay National Wildlife Refuge. Use is measured as the percentage of total telemetry locations of a snake that occur in a given grid cell.....	84
13. Movement Map for subject AP-1 (male) in the natural marsh at Back Bay National Wildlife Refuge. The capture and release site is shown as a square, movement locations are shown as dots, and the hibernaculum is shown as a circled "H." Dates are shown for locations. Unlabeled areas on map shown by curved lines indicate low-lying marsh shrubs.....	93
14. Movement map for subject AP-2 (male) in the natural marsh at Back Bay National Wildlife Refuge. The capture and release site is shown as a square, movement locations are shown as dots, and the hibernaculum is shown as a circled "H." Dates are shown for locations. Unlabeled areas on map shown by curved lines indicate low-lying marsh shrubs.....	94
15. Movement map for subject AP-3 (female) in the natural marsh at Back Bay National Wildlife Refuge. The capture and release site is shown as a square, movement locations are shown as dots, and the hibernaculum is shown as a circled "H."	

FIGURE

Page

Dates are shown for locations. Unlabeled areas on map shown by curved lines indicate low-lying marsh shrubs.....	95
16. Movement map for subject AP-4 (female) in the anthropogenic marsh at Back Bay National Wildlife Refuge. The capture and release site is shown as a square, movement locations are shown as dots, and the hibernaculum is shown as a circled "H." Dates are shown for locations. Unlabeled areas on map shown by curved lines indicate forested sites.....	96
17. Movement map for subject AP-5 (female) in the anthropogenic marsh at Back Bay National Wildlife Refuge. The capture and release site is shown as a square, movement locations are shown as dots, and the hibernaculum is shown as a circled "H." Dates are shown for locations. Unlabeled areas on map shown by curved lines indicate forested sites.....	97
18. Distance moved per day (biweekly mean) for subject AP-1 (natural marsh, male) at Back Bay National Wildlife Refuge. The chart shows biweekly movements against Julian date both prior to ingress into the hibernaculum, and after egress from the hibernaculum. Season and year are given.....	102
19. Distance moved per day (biweekly mean) for subject AP-2 (natural marsh, male) at Back Bay National Wildlife Refuge. The chart shows biweekly movements against Julian date both prior to ingress into the hibernaculum, and after egress from the hibernaculum. Season and year are given.....	103
20. Distance moved per day (biweekly mean) for subject AP-3 (natural marsh, female) at Back Bay National Wildlife Refuge. The chart shows biweekly movements against Julian date both prior to ingress into the hibernaculum, and	

FIGURE

Page

after egress from the hibernaculum. Season and year are given.....	104
21. Distance moved per day (biweekly mean) for subject AP-4 (anthropogenic marsh, female) at Back Bay National Wildlife Refuge. The chart shows biweekly movements against Julian date both prior to ingress into the hibernaculum, and after egress from the hibernaculum. Season and year are given.....	105
22. Distance moved per day (biweekly mean) for subject AP-5 (anthropogenic marsh, male) at Back Bay National Wildlife Refuge. The chart shows biweekly movements against Julian date both prior to ingress into the hibernaculum, and after egress from the hibernaculum. Season and year are given.....	106
23. Body and environmental temperature profiles for subject AP-1 (natural marsh, male) at Back Bay National Wildlife Refuge. Profiles show weekly mean temperatures for eight weeks—two weeks prior to and after ingress into the hibernaculum, and two weeks prior to and after egress from the hibernaculum. Ingress and egress dates, as well as body, air, surface, and soil temperatures for ingress and egress dates are shown.....	112
24. Body and environmental temperature profiles for subject AP-2 (natural marsh, male) at Back Bay National Wildlife Refuge. Profiles show weekly mean temperatures for eight weeks—two weeks prior to and after ingress into the hibernaculum, and two weeks prior to and after egress from the hibernaculum. Ingress and egress dates, as well as body, air, surface, and soil temperatures for ingress and egress dates are shown.....	113
25. Body and environmental temperature profiles for subject AP-3 (natural marsh, female) at Back Bay National Wildlife Refuge. Profiles show weekly	

FIGURE

Page

mean temperatures for eight weeks--two weeks prior to and after ingress into the hibernaculum, and two weeks prior to and after egress from the hibernaculum. Ingress and egress dates, as well as body, air, surface, and soil temperatures for ingress and egress dates are shown.....	114
26. Body and environmental temperature profiles for subject AP-4 (anthropogenic marsh, female) at Back Bay National Wildlife Refuge. Profiles show weekly mean temperatures for eight weeks--two weeks prior to and after ingress into the hibernaculum, and two weeks prior to and after egress from the hibernaculum. Ingress and egress dates, as well as body, air, surface, and soil temperatures for ingress and egress dates are shown.....	115
27. Body and environmental temperature profiles for subject AP-5 (anthropogenic marsh, male) at Back Bay National Wildlife Refuge. Profiles show weekly mean temperatures for eight weeks--two weeks prior to and after ingress into the hibernaculum, and two weeks prior to and after egress from the hibernaculum. Ingress and egress dates, as well as body, air, surface, and soil temperatures for ingress and egress dates are shown.....	116
28. Snake sightings by visitors at Back Bay National Wildlife Refuge during 1996 and 1997. The categories shown include copperheads, a species reported quite often at the Refuge, but which does not occur there.....	117
29. Snake sightings by hunters at Back Bay National Wildlife Refuge during 1997. The categories shown include copperheads, a species reported quite often at the Refuge, but which does not occur there.....	118

INTRODUCTION

The eastern cottonmouth (*Agkistrodon p. piscivorus*) reaches its northernmost limit in southeastern Virginia. Aside from a study of genetic variation in cottonmouth populations in Virginia (Merkle, 1985), a study of the reproductive ecology of the cottonmouth in its northernmost population (Blem, 1981), and a brief comparative ecology that included a small sample from southeastern Virginia (Blem and Blem, 1995), there has been no attempt to quantify the population ecology or behavior of this animal in southeastern Virginia. Large numbers of cottonmouths are reported to occur at Back Bay National Wildlife Refuge (BBNWR), but no studies have been designed to study the populations there.

Large-scale ecological studies of cottonmouths have been carried out in other locations where it commonly occurs, though these studies involved different subspecies. Carr (1937), Allen and Swindell (1948), and Wharton (1969) have studied the ecology of Florida cottonmouths (*Agkistrodon piscivorus conanti*), and Barbour (1956) and Burkett (1966) published on the ecology of the western cottonmouth (*Agkistrodon p. leucostoma*).

This study had several objectives, including both ecological and methodological questions. The specific objectives were: (1) to determine the proper sampling protocols and statistical estimation procedures needed to estimate population sizes; (2) to evaluate cottonmouth feeding ecology through sampling of stomach contents; (3) to compare morphological characteristics of cottonmouths from different areas of BBNWR; (4) to examine movement patterns and activity ranges, the influence of temperature, and hibernaculum use for cottonmouths; (5) to evaluate habitat use by the investigation of vegetation composition and community structure for sites used by individuals in both radiotelemetric and mark-recapture studies (This objective included the development of

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proper sampling protocols and statistical treatment of habitat data.); (6) to document the behavior and occurrence of cottonmouths at BBNWR by direct observation and through reports from visitors and hunters, and (7) to suggest management strategies for cottonmouth populations at BBNWR.

Systematics and Ecology of Agkistrodon piscivorus

Systematics and Distribution.—*Agkistrodon piscivorus* (Lacépède) contains: (1) *Agkistrodon p. piscivorus* (eastern cottonmouth), ranging from southeastern Virginia to southern Georgia, (2) *A. p. conanti* (Florida cottonmouth), ranging from southern Georgia to southernmost Florida, including the upper Florida Keys, and (3) *A. p. leucostoma* (western cottonmouth), ranging from Alabama to eastern Texas. Only the nominate subspecies occurs in Virginia, where most populations are clustered east of Suffolk (Gloyd and Conant, 1990; Mitchell, 1994). The North American species of *Agkistrodon* is most likely derived from an Asian member of the genus. The first *Agkistrodon* in North America probably crossed the Bering land bridge in tropical deciduous or mixed forest in the Middle Tertiary, about 24 MYBP (Van Devender and Conant, 1990).

Description.—The cottonmouth is a relatively large, heavy-bodied, dark-colored pit viper with broad, hourglass-shaped dorsal bands and a markedly triangular head (Ernst, 1992; Mitchell, 1994). The dorsal ground color is yellow-olive to dark brown or black, and the venter is tan to gray and heavily patterned with dark blotches (Mitchell, 1994). Some individuals possess a light-bordered, dark cheek stripe or dark bars on the rostrum. This is most notable in *A. p. conanti* (Ernst, 1992). Juveniles are lighter in color than adults, with a sulfur-yellow tail tip. Crossbands are conspicuous in juveniles, but become obscured with age (Ernst, 1992).

Adult cottonmouths show pronounced sexual dimorphism, with males considerably longer and heavier than females (Mitchell, 1994). In Virginia snout-vent length (SVL) of

males ranged from 755-1034 mm (\bar{x} = 976.9 mm; n = 51) and mass ranged from 384-1700 g (\bar{x} = 1035.0 g). For females SVL ranged from 660-940 mm (\bar{x} = 275.9 mm; n = 43) and mass was 435-700 g (\bar{x} = 560.3 g; Mitchell, 1994). In southeastern Virginia Blem and Blem (1995) found mean SVL to be 630.0 mm for 36 males, and 548.1 mm for 18 females. Males had substantially longer tails than did females (\bar{x} = 117.4 mm vs. 99.1 mm) but there was little difference in head length (\bar{x} = 38.97 mm for males vs. 36.47 for females) or head width (\bar{x} = 28.94 mm for males vs. 27.12 for females; Blem and Blem, 1995). Maximum adult size has been reported as 1880 mm by Conant and Collins (1991) and 1892 mm by Ernst (1992). Mitchell (1994) examined nine Virginia neonates and reported that the SVL ranged from 221-237 mm (\bar{x} = 227.9 mm) and mass ranged between 14.5-18.0 g (\bar{x} = 16.3 g).

Reproductive biology.—Mating of *Agkistrodon piscivorus* generally occurs in the spring, but may take place sporadically in other warm months (Wharton, 1966). Male cottonmouths are known to perform a combat ritual (Carpenter and Gillingham, 1990; Gloyd and Conant, 1990; Mitchell, 1994), and defense of mates was reported by Martin (1984). In Virginia the smallest sexually mature male was 755 mm SVL, and the smallest sexually mature female was 660 mm SVL (Mitchell, 1994). Given the relationship between size and age found by Blem and Blem (1995), sexual maturity is attained at an age of approximately three years in cottonmouths. Ovulation occurs in late May in Virginia, and embryos develop through September (Blem, 1981). Cottonmouths are viviparous, and Virginia females generally give birth to litters of 5-9 individuals (\bar{x} = 7.7; Blem, 1981) in September (Mitchell, 1994).

Gloyd and Conant (1990) suggest a biennial to triennial cycle of reproduction for the cottonmouth. Blem (1981) points out that although a biennial reproductive cycle was expected, with 50% of females giving birth in any year, he found 83% of the females he collected to be gravid; however, this high percentage may reflect positive bias due to increased basking behavior of gravid females, a behavior not mentioned by the author.

Behavior.--Some authors (Ernst, 1992; Gloyd and Conant, 1990; Mitchell, 1994) suggest that cottonmouths are generally not as aggressive as reported in older manuscripts (Army Air Force, 1945; United States Navy, 1966), although they often remain in place and gape their jaws widely when approached, showing the white interior of the mouth. Cottonmouths will readily strike when molested. Wharton (1969) demonstrated that aggressive behaviors were more readily evident at lower temperatures (between 4.4 C and 15.6 C), whereas escape behaviors were much more common at higher temperatures. Goode and Duvall (1989) studied the relationship between body temperature and defensive behavior in free-ranging prairie rattlesnakes (*Crotalus v. viridis*). The literature concerning the relationships between temperature and behavioral ecology has been discussed by Ford and Burghardt (1993).

Cottonmouths are diurnal during the spring and fall and become predominantly nocturnal during the summer months (Ernst, 1992). During the winter, snakes retreat to hibernacula ranging from hollow stumps to rock escarpments. Some cottonmouths have been reported to aggregate for hibernation (Dundee and Burger, 1948; Wharton, 1969).

Conservation and Management.--In Virginia cottonmouths are not currently listed as a species of special concern (Mitchell, 1994). However, like many other organisms cottonmouths are sensitive to the loss of wetland habitat and have undoubtedly lost valuable parts of their range as a consequence of wetland destruction and urbanization. Additionally, many potential predators of cottonmouths are abundant at BBNWR including red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), great blue herons (*Ardea herodias*), largemouth bass (*Micropterus salmoides*), and even ghost crabs (*Ocypode quadrata*; Cross and Marshall, 1998; Gloyd and Conant, 1990; Mitchell, 1994).

Habitat

The concept of habitat is difficult to define. Daubenmire (1968) states that "habitat is usually used to denote a rather specific kind of living environment, i. e., a constellation of interacting physical and biological factors which provide at least minimal conditions for one organism to live or for a group to appear together." This definition describes an animal's "macrohabitat." To define the area used by an animal in more specific terms, researchers often discuss the suite of habitat characteristics used by an organism in its immediate environment, the "microhabitat" (Ricklefs, 1993). The concept of microhabitat will be used in the analyses undertaken in this investigation.

Accurate measurement and assessment of microhabitat are important considerations when studying the ecology and management of wildlife (Alldredge and Ratti, 1986; Johnson, 1980; Morrison et al., 1992). The information concerning the relationship between wildlife species and their habitats provides basic life-history information that may be important for the conservation and management of an organism (Carey, 1981; Morrison et al., 1992).

Microhabitat analyses have been based upon the niche gestalt theory (James, 1971; North and Reynolds, 1996), which was derived from the multidimensional niche theory (Hutchinson, 1957; North and Reynolds, 1996; Reinert, 1992, 1993). According to this idea, the niche occupied by an organism is a complex space that contains the necessary environmental conditions for a species' survival (Hutchinson, 1957; Morrison et al., 1992; Reinert, 1992, 1993). In general, an animal's multidimensional niche is derived from a multivariate analysis of habitat, dietary, and life-history variables across a range of sites where the animal is found (North and Reynolds, 1996; Shugart, 1981).

Habitat Use and Selection by Snakes

Snakes are often secretive and therefore difficult to find in their natural environment (Reinert 1992, 1993). As a result, habitat use by snakes has not been accorded the attention given to taxa that are more easily seen, trapped, or otherwise observed (Gregory et al., 1987; Reinert, 1992, 1993). Historically, habitat use by snakes was ascertained by intensive mark-recapture studies in which many snakes were captured multiple times (King, 1986; Plummer, 1981, 1997; Wharton, 1969). The increased availability and use of radiotelemetry equipment, however, has led to a tremendous increase in our understanding of habitat use by snakes (Reinert, 1984a,b, 1992, 1993).

Habitat use by snakes may reflect various factors, and a thorough review of the pertinent literature can be found in Reinert (1993). Foraging has been shown to influence habitat use by Arafura file snakes (*Acrochordus arafurae*; Shine and Lambeck, 1985) and the Florida cottonmouth (*Agkistrodon piscivorus conanti*; Wharton, 1969). The digestive state of the animal may also play an important role (Gibson et al., 1989; Lutterschmidt and Reinert, 1990; Petersen, 1995). Shedding, or sloughing of the skin, was shown to cause a shift in habitat use and movement patterns in the copperhead snake (*Agkistrodon contortrix*; Petersen, 1995). Additionally, social interactions, particularly during the mating season, may cause habitat shifts (Gregory et al., 1987; Lillywhite, 1985).

Several cues may play a factor in habitat selection (Reinert, 1993). Among these are temperature, which influences thermoregulatory behavior of the animal (Huey, 1991), learning, as evidenced by repeated use of the same locations over time (Burger and Zappalorti, 1988; Petersen, 1995), and identification of structural features of desirable habitat, which may be learned over time (Reinert, 1984a, b; Reinert and Zappalorti, 1991).

The cottonmouth, the only semi-aquatic member of the *Agkistrodon* complex, has been reported to occupy nearly any type of habitat where water is found, from drainage ditches in suburbs to brackish coastal wetlands, cypress swamps, bayous, streams, rivers,

and forested wetlands (Gloyd and Conant, 1990; Conant and Collins, 1991; Ernst, 1992; Mitchell, 1994).

Modeling Habitat Use

Most of the methods common to modeling habitat use have focused on the idea of use sites (those sites known by observation to be used by an animal) versus available or non-use sites (randomly selected sites where it is assumed, for the purposes of modeling, that the animal does not occur during the course of the investigation). Many papers have been published on this technique (Alldredge and Ratti, 1986; Hobbs and Hanley, 1990; Johnson, 1980; Marcum and Loftsgaarden, 1980; Porter and Church, 1987; Thomas and Taylor, 1990). This type of modeling has historic prominence in the snake literature (Burger and Zappalorti, 1988; Reinert and Kodrich, 1982; Petersen, 1995; Reinert 1984a, b; Reinert and Zappalorti, 1988). Other methods include linear regression models (Morrison et al., 1987) and Habitat Suitability Index Modeling (HSI models; U. S. Fish and Wildlife Service, 1981).

Many problems exist with current methods, particularly with multivariate techniques (North and Reynolds, 1996). One widely used technique, discriminant function analysis, relies upon assumptions of multivariate normality and constant covariance structure across all sites, an assumption rarely met with ecological data (Johnson, 1981; Noon, 1986; North and Reynolds, 1996). Many other multivariate techniques are also weakened by these assumptions (see Morrison et al., 1992), though some nonparametric adaptations are possible (e.g., nonparametric discriminant function analysis). It is surprising, then, that these very techniques have been central to many snake studies.

A method that does not rely upon strict multivariate assumptions is greatly needed. Polytomous logistic regression (PLR) models site use-intensity from radiotelemetry data, hence eliminating the need for ancillary data on non-use sites. The PLR technique makes

no assumptions about normality or common covariance structure, making it appealing for habitat modeling (Hosmer and Lemeshow, 1989; McCullagh and Nelder, 1989; North and Reynolds, 1996). The use of PLR for modeling snake habitat use may provide a useful alternative to traditional modeling efforts and is explored further in this investigation.

Population Estimation

The estimation of animal abundance is often central to the study of a population under ecological investigation (Blower et al., 1981; Menkens and Anderson, 1988; Otis et al., 1978; Pollock et al., 1990; Skalski and Robson, 1992; Strong et al., 1994). Many techniques and methodologies have been proposed for population estimation (see Seber, 1982, 1986, 1992 for thorough reviews; Buckland et al., 1993; Krebs, 1989; Skalski and Robson, 1992). Mark-recapture methods are by far the most common technique for estimating numbers of mammals and fishes (Burnham et al., 1987; Hallet et al., 1991; Seber, 1982; Skalski and Robson, 1992), whereas distance methods are common for estimating numbers of birds (Buckland et al., 1993).

Mark-recapture techniques are carried out by capturing, marking, and subsequently releasing individuals from a given population, waiting an established amount of time, and then resampling from the population to see what fraction of the recaptured individuals carry marks (Krebs, 1989; Seber, 1982). Mark-recapture estimation techniques can be used for populations that are either closed to births and deaths (immigration and emmigration are generally considered to be negligible during the sampling period) or open to births and deaths (Jolly, 1965; Otis et al., 1978; Seber, 1965, 1982, 1986, 1992). Several assumptions are necessary in order to model the population correctly: all animals have the same probability of first capture, marking does not affect subsequent capture probabilities, animals do not lose marks, and marked individuals randomly disperse in the population after being released (Krebs, 1989; Otis et al., 1978;

Nichols and Pollock, 1988; Pollock et al., 1990). Several computer-intensive estimation procedures allow for heterogeneity and behavioral responses in the probability of trapping, (Otis et al., 1978) as well as for estimating tag losses (Robinson-Cox, 1998; Seber, 1982).

Distance methods are carried out either by a line-transect method (or a derivative thereof) or by point counts (Buckland et al., 1993). In these types of sampling schemes, the distance to a study animal and/or its angle from a transect line must be estimated fairly accurately. Given these constraints the bulk of the literature for these methods is for estimating bird densities, though the densities of most vertebrate groups and some insects have been estimated by distance sampling (see Buckland et al., 1993 for a thorough review). The difficulty inherent in capturing some species of snakes limits the use of this technique in most snake population studies.

Estimation of Snake Abundance

The estimation of snake abundance is a difficult task. Parker and Plummer (1987: p. 253) offer four reasons for this: "(1) Snakes are often inconspicuous and nocturnal; (2) many snakes have extended periods of inactivity; (3) apparent population densities often are low; (4) the relatively extensive and irregular movements of some snakes make it difficult to define the boundaries of a population." The apparent low densities of snakes in most ecological investigations is evident when reviewing the literature (Parker and Plummer, 1987, pp. 255-258).

The primary difficulty in estimating snake numbers and densities is low capture and recapture rates, with the latter contributing to severe mathematical limitations (Parker and Plummer, 1987; Turner, 1977). As an extreme example, Kropach (1975) marked nearly 1000 *Pelamis platurus* near Panama and never recaptured a single individual during subsequent sampling. *P. platurus* however, is a pelagic marine species. Even in the

extensive field investigations of *Agkistrodon contortrix* by Fitch (1960), only 11 individuals of 492 marked were recaptured during a ten-year period. However, there are some instances where snake densities, and hence recapture rates, are high. Most of these populations are found on islands (King, 1986; Wharton, 1969), in restricted ecological localities (Voris, 1985), or at communal hibernacula (Gregory, 1974; Woodbury, 1951).

Even with the difficulties introduced by low recapture rates, mark-recapture techniques remain the primary estimation tool for herpetological studies, with simple two-capture Lincoln-Peterson estimation being most popular (Fitch, 1960; King, 1986; Parker, 1976; Turner, 1977; Parker and Plummer, 1987; Plummer, 1997; Voris, 1985;). This trend will likely continue given the prominence of this technique in studies of other vertebrate groups and the consequent theoretical work in this area (Seber, 1982). Additionally, mark-recapture records also are quite useful for monitoring morphological measures of individual growth (such as body size and mass) over time, for estimating activity areas, and for investigating feeding habits (Parker and Plummer, 1987; Wharton, 1969). The trade-off granted by obtaining information on these parameters is often justifiable even if accurate population estimates cannot be made.

Trophic Ecology and Behavior

Foraging ecology of the cottonmouth, and of snakes in general, is most often investigated indirectly by making assumptions based on results from gut content analyses (Savitzky, 1992). Analyses of cottonmouth gut contents in early ecological investigations suggested that the snakes took prey both on and under the water surface and on land (Barbour, 1956; Clark, 1949). Field and laboratory investigations on the foraging ecology of the cottonmouth confirmed these suggestions. Allen and Swindell (1948) report observations from both the field and laboratory. Their investigations showed that the cottonmouth feeds mostly on aquatic prey, and that foraging was restricted to the cooler

times of the day and at night. Wharton (1969) confirmed that feeding occurred mostly by active foraging during the nighttime hours. Bothner (1974) reported cottonmouth foraging in drying pools. In the laboratory Savitzky (1992) studied aquatic foraging behavior of the cottonmouth and found that it was less adept than other aquatic snakes at catching fish. Wharton (1960) reported caudal luring by young cottonmouths, which waved their sulfur yellow-tipped tails in front of frogs.

Allen and Swindell (1948) suggested that the short fangs of cottonmouths restricted them to foraging on mostly furless prey. The mean length of cottonmouth fangs, however, are longer than those of copperhead snakes, which are known to feed on rodents (Ernst, 1982; Fitch, 1960). Chiszar and his colleagues (1979, 1985, 1986) have investigated cottonmouth foraging extensively in the laboratory, both in terms of the formation of chemosensory search images and in trailing behavior. They found that the snakes were adept at finding rodents after a strike and release of the prey, but that fish prey were held rather than released. Allen and Swindell (1948) and O'Connell et al. (1981) reported that fish were held after striking. This may be an advantage when feeding on prey that could easily swim away after a strike (Bothner, 1974; Gloyd and Conant, 1990). Savitzky (1993) suggests that mechanisms associated with capture and rapid swallowing of piscivorous prey are favored by natural selection. An extensive study of capturing and handling fish by cottonmouths is found in Savitzky (1992). Kardong (1975, 1977, 1982) defined several foraging phases of the cottonmouth with mouse prey items in the laboratory. He found that some mice were retained in the jaws after the strike, but that others were released. Retention of prey has been suggested to result from nonoverlapping central nervous system representations of search images of aquatic and rodent prey (Chiszar et al., 1985; O'Connell et al., 1981).

Though fish and frogs make up a majority of the reported food items of the cottonmouth, the snakes are known to eat a wide range of prey, and often mistakenly eat nondigestible items as well, such as rocks and sticks (Allen and Swindell, 1948; Ernst,

1992; Gloyd and Conant, 1990; Mitchell, 1994; Savitzky, 1992; Wharton, 1969). A review of reports containing lists of preferred food items for several snakes, including the cottonmouth, is provided by Mushinsky (1987) and Savitzky (1992) reviewed the literature concerning habitats and food items of the cottonmouth. Reported prey items include frogs (*Rana* spp.), shrews (*Cryptotis parva*), hispid pocket mice (*Perognathus hispidus*), Carolina chickadees (*Parus carolinensis*), pied-billed grebes (*Podilymbus podiceps*), many species of fishes, many species of snakes (including other cottonmouths), turtles, and insects (mostly Coleoptera; Brown, 1979; Collins, 1980; Collins and Carpenter, 1970; Ernst, 1992; Gloyd and Conant, 1990; Klimstra, 1959; Leavitt, 1956; Mitchell, 1994; Wharton, 1969). Wharton (1969) reported that the majority of cottonmouths on Sea Horse Key, Florida were feeding on carrion (fish dropped from heron and egret nests). Many of the snakes that he examined also contained mud, sticks, rocks, and plant matter, which he attributed to the ravenous feeding behavior of these animals.

Though cottonmouths have been shown to eat almost anything, many studies examining the feeding ecology in these snakes have demonstrated that they feed less frequently than anticipated given their purported voracious appetites. This is evidenced by a high percentage of empty stomachs. Wharton (1969) found that 89.5% of the stomachs that he examined were empty. This ranged from 69.3-97.5% depending on the time of year, with the lowest percentage of empty stomachs found during the active summer months. Additionally, Barbour (1956) reported only 25% of his snakes with food items, Collins and Carpenter (1970) reported only 57%, and Blem and Blem (1995) only 16%; however, Klimstra (1959) reported that 81% of the snakes he examined contained food.

Activity Ranges and Movements

Movements of individuals over time have been studied extensively for many snake species (Gregory et al., 1987; Reinert, 1993; White and Garrott, 1990). However, it is

often difficult to understand fully what cues are used by an animal and the motivation underlying the choice of one area over another. Gregory et al. (1987) offer three reasons why it is difficult for researchers to grasp where and why animals move: "(1) we have an incomplete understanding of an animal's needs, (2) we seldom measure the availability of required resources, and (3) given that we could measure resource availability, our perception of availability may not be the same as that of the animal." Modeling habitat use and availability (see *Modeling Habitat Use*) may offer partial answers to numbers (1) and (2), but modeling necessarily requires that the researcher choose measurements deemed important to the species being modeled, which may be little more than a best guess of what the species perceives or requires. Though why an animal moves is not always answerable, movement itself is a measurable entity.

Factors affecting movements.—Resource availability undoubtedly plays a major role in the the movements and activity ranges of snakes (Gregory et al., 1987). Availability of a water source for semi-aquatic snakes has been shown to affect movements (Godley, 1980; Wharton, 1969). Wharton (1969) showed that cottonmouths on Sea Horse Key, Florida gathered under a heron rookery, where they fed on falling fish dropped from above. Hand in hand with resource availability is the influence of habitat structure. Topography (Brown et al., 1982; Carpenter, 1952) may play an important role in habitat selection and movements by limiting snakes to certain areas within a larger region. Natural edge effects (such as riparian habitats) may affect snake movement patterns (Madsen, 1984; Plummer, 1981, 1997), as might man-made structures. Petersen (1995), for example, found that three of his radiotelemetry subjects spent a large percentage of their time in anthropogenic habitats.

Sex and reproductive activities have been linked to differential movement patterns in snakes, though Gregory et al. (1987) caution that no definite trend is obvious from the literature. Madsen (1984) found that females of the grass snake (*Natrix natrix*) in southern Sweden occupied larger areas than did males, and Gannon and Secoy (1985)

found this to be true for prairie rattlesnakes (*Crotalus viridis*) in Saskatchewan, Canada. On the other hand, Petersen (1995) found that male copperheads (*Agkistrodon contortrix*) used greater areas than females. These differential movements may be linked to mate-searching activities (Duvall et al., 1985) and movements to parturition sites (Parker and Brown, 1972). Additionally, there is evidence that gravid females might have different movement patterns than non-gravid females in the timber rattlesnake (*Crotalus horridus*; Brown et al., 1982; Reinert and Zappalorti, 1988).

Thermoregulatory behavior has been shown to affect movement patterns (Lillywhite, 1985). Differential activity patterns due to temperature most often lead to decreased activity during the warmest parts of the active season, and thereby cause a change from a diurnal to a nocturnal activity pattern. This has been shown in many snakes, including copperheads (Petersen, 1995; Sanders and Jacobs, 1980), cottonmouths (Savitzky, 1992; Wharton, 1969), rattlesnakes (Landreth, 1973), smooth earth snakes (*Virginia valeriae*), scarlet snakes (*Cemophora coccinea*), and southeastern crowned snakes (*Tantilla coronata*; Gibbons and Semlitsch, 1982). Snake thermal ecology is reviewed in Peterson et al. (1993).

Activity ranges and estimation.—Activity range is broadly defined as that area utilized by an individual in a defined time interval. This term is often used synonymously with "home range," a term initially employed by Burt (1943). Gregory et al. (1987) found in snake literature that at least six terms had been used to describe the activity range. In the present study the activity range is understood to be that area used by the snake during the active season.

Measurements of activity area are either discerned from mark-recapture studies (e.g., Wharton, 1969) or from radiotelemetry (White and Garrott, 1990). Many measures are available for estimating activity areas, from simple geometric measures to elaborate statistical techniques. Extensive descriptions of methods and examples can be found in Mohr and Stumpf (1966) and White and Garrott (1990). The use of time series analyses

for analyzing seasonal variations in habitat usage for snake data was described by Reinert (1992). The most common methods currently used in snake studies are the area enclosed by the minimum convex polygon (MCP; Mohr, 1947), and the area enclosed by the 95% isopleth of the harmonic mean (HM; Dixon and Chapman, 1980; Reinert, 1992). The use of HM estimates for activity range size has been shown to lead to biased results in some cases (Worton, 1989, 1995).

Gregory et al. (1987) cite an unpublished report that activity ranges in snakes range from 0.0009-34.5 ha. A tabular survey for movements and activity range size was compiled by Macartney et al. (1988). Petersen (1995) found that MCP activity ranges in female copperheads ranged from 1.55-5.17 ha and for males 3.22-17.66 ha. Wharton (1969) found that cottonmouths on Sea Horse Key, Florida had activity range areas similar to the snakes on the mainland, with males averaging 0.174 ha and females 0.142 ha.

Hibernation

Hibernation in reptiles has been studied extensively in terms of physiology (Gregory, 1982). The factors affecting movement into and out of hibernacula are broadly correlated with the temperature profiles of the shallow and deep soil layers around hibernacula (Sexton and Hunt, 1980). That is, as the shallower layers become colder than deeper layers, snakes should enter hibernacula, and as that temperature scheme reverses, snakes should egress (Sexton et al., 1992).

In order to test the thermal reversal prediction and examine general latitudinal trends, Sexton et al. (1992) submitted a questionnaire to 147 potential cooperators in the contiguous 48 United States. They obtained information on 45 different species of snakes. The questionnaire divided hibernation behavior into five categories, ranging from hibernation in interspecific, communal underground dens to no hibernation behavior (i.e.

snakes were active all year;). Additionally, soil temperature profiles were examined in their study.

Sexton et al. (1992) found that cottonmouths exhibited all five categories of hibernation behavior, varying according to latitude. Cottonmouths in Missouri and Illinois, for example, were found in intraspecific, communal dens, whereas the most southern populations exhibited either no hibernation behavior or used only temporary cover during cold times of the year. Wharton (1969), however, found communal denning in Florida). Using their information along with soil temperature profiles, Sexton et al. (1992) suggested that use of underground, communal hibernacula should occur above 38° latitude, and that solitary hibernacula, use of temporary cover, and full winter-season activity should occur below 38° latitude.

Movements to and from hibernacula are well documented and often involve large movements (Gibbons and Semlitsch, 1987). Site fidelity has been shown in several species and is summarized in Gibbons and Semlitsch (1987). Activity during hibernation may be absent in colder climates (Gibbons and Semlitsch, 1987), but basking behavior during sunny days has been documented for cottonmouths (Wharton, 1969) and prairie rattlesnakes (Jacob and Painter, 1980). Egress from hibernation seems to be correlated with temperature rather than date (Gibbons and Semlitsch, 1987).

MATERIALS AND METHODS

Study Site

This study was conducted at Back Bay National Wildlife Refuge (BBNWR) in Virginia Beach, Virginia. The Refuge headquarters, located at N36°40'19":W75°54'55", sits in the main area of BBNWR (Fig. 1). The Refuge is bordered on the north by Little Island Park and on the south by False Cape State Park. The Refuge was established in 1938 (BBNWR Station Management Plan, July 1993). Approximately 11000 ha of marsh was included in the 1938 acquisition, and in 1939 an additional 11400 ha of open water within Back Bay was closed to waterfowl hunting. Since that time a total acquisition area of 27200 ha has been approved (BBNWR Station Management Plan, July 1993). Most of the newly approved acquisition land is in the area surrounding Sandbridge Beach, Virginia Beach, Virginia, and was not included in this study. The Refuge and the surrounding acquisition area contain a large diversity of both plant and animal life (see BBNWR Station Management Plan, July 1993; USFWS publication RL-51510).

Two major areas of the Refuge were compared in this study. The first extends from the area surrounding the headquarters and north to the northern border (referred to herein as the natural marsh system), and the other lies south of the headquarters and extends to the northern border of False Cape State Park (referred to herein as the anthropogenic marsh system). Sampling for this investigation treated the natural and anthropogenic marshes as separate systems. There is only one replicate for each marsh system, weakening the inference of causal factors associated with different areal treatments, although differences between the two habitats can be inferred from the data obtained.

Natural marsh system.—The natural marsh system of BBNWR is dominated by low, dense vegetation. Black needlerush (*Juncus roemerianus*), arrowhead (*Sagittaria*

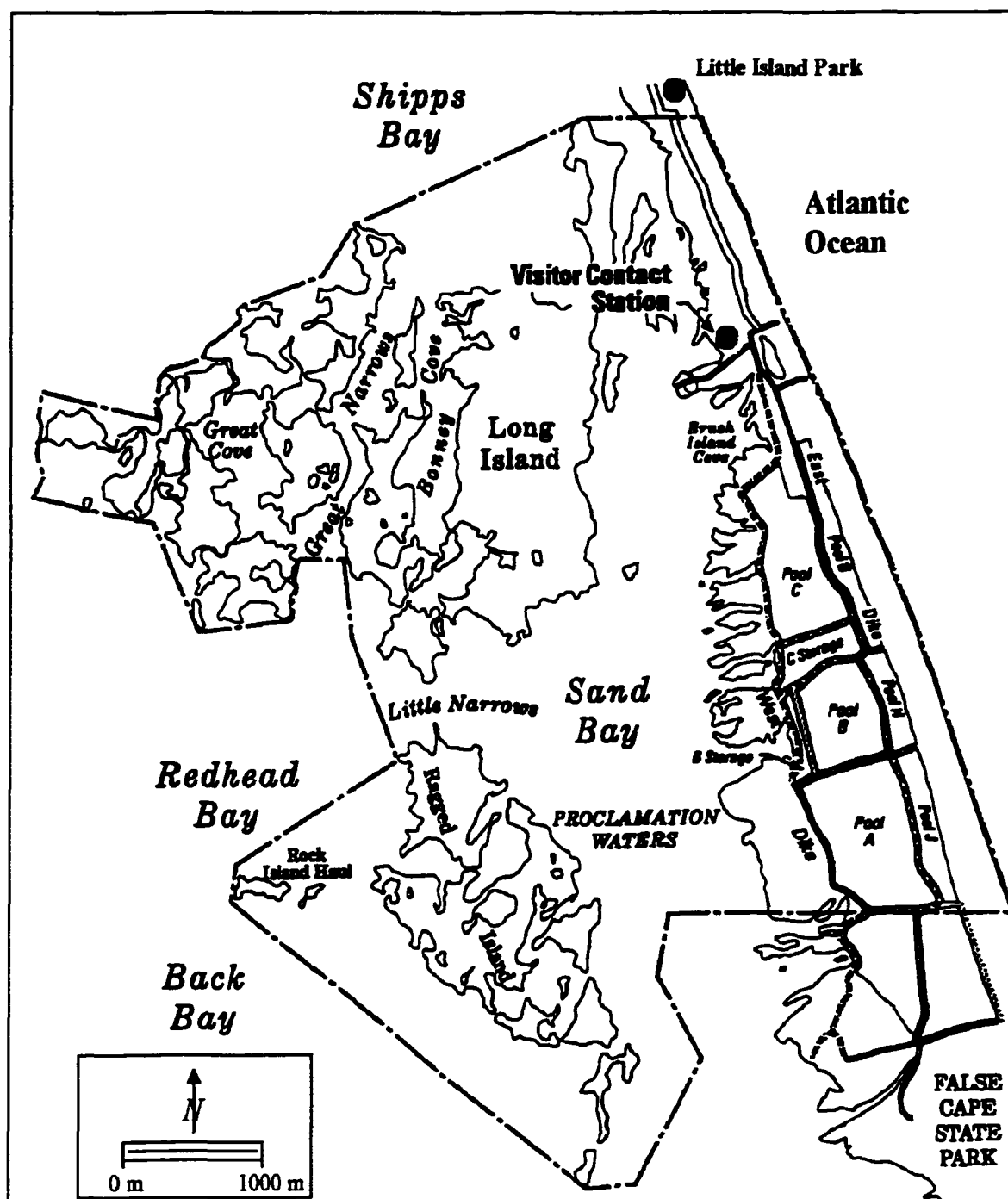


FIG. 1.--Area map for Back Bay National Wildlife Refuge showing both the natural marsh (area north of the Visitor Contact Station, Long Island, and Ragged Island) and the anthropogenic marsh (area south of the Visitor Contact Station). The Refuge is bordered by Little Island Park to the north and by False Cape State Park to the south. Refuge boundaries are shown by the dash-dot line.

spp.), cattail (*Typha* spp.), cordgrass (*Spartina cynosuroides*), and many other marsh species are common throughout the northern marsh. Low woodlands and shrublands are dominated by American holly (*Ilex opaca*), wax myrtle (*Myrica cerifera*), greenbrier (*Smilax* spp.), and red maple (*Acer rubrum*). In addition, many dune grasses are found in this area, including sea rock (*Cakile edentula*), sea oats (*Uniola paniculata*), and spurge (*Euphorbia polygonifolia*).

Several roadside drainage ditches, naturally occurring ponds, and an artificial pond used for educational purposes provide cottonmouth habitat. The shoreline along Back Bay also provides ideal habitat. The open bay is occasionally traversed by cottonmouths, and two large islands, Long Island and Ragged Island, were investigated for the presence of snakes. The open water of Back Bay permits passage to islands or to different areas along the Bay shore. Approximately 1200 ha, including the two aforementioned islands, made up the study area of the northern marsh (Fig. 1).

Anthropogenic marsh system.—The anthropogenic marsh system is maintained for the management of migratory waterfowl and shorebirds at BBNWR, and it is managed as a series of impoundments. Manipulation of water levels via water control structures is a major tool for managing the impoundments, together with mowing, disking and root raking, and burning (Fredrickson and Taylor, 1982).

Vegetation in the managed impoundment consists of beggar's tick (*Bidens* spp.), black needlerush, spike rush (*Eleocharis* spp.), three-square (*Scirpus americanus*), water-hyssop (*Bacopa* spp.), pennywort (*Centella asiatica*), and many others. Along the western edge of this area is a relatively undisturbed forest with an overstory of loblolly pine (*Pinus taeda*), laurel oak (*Quercus laurifolia*), and live oak (*Q. virginianus*), and an understory dominated by blueberry (*Vaccinium* spp.), poison ivy (*Toxicodendron radicans*) and greenbrier (*Smilax* spp.).

The anthropogenic marsh system is a set of pools running north to south between the Atlantic Ocean dune system and Back Bay. Along the edges of the managed pools are

deep ditches and levees that presumably provide dispersal routes for snakes and their prey (including frogs and fishes). Those structures were monitored closely. Also, snakes could be found on the interior pools in areas of standing water. Approximately 1900 ha of the anthropogenic marsh system was monitored in this study (Fig. 1). Seasonal alteration of habitat by Refuge staff altered the accessibility of different areas of the pools throughout the study.

Capture and Measurements

All snakes were captured using snake tongs (Azul Reptile Snare, Forestry Suppliers, Inc., Jackson, Mississippi) to reduce the chance of accidental bites to the investigator. Snakes were placed into a plastic squeeze box equipped with a foamed rubber pad and plexiglass (modified from Quinn, 1974) and were secured for measurements. A grease pencil was used to mark the length of snakes on the plexiglass from snout tip to tail tip. Additionally, marks were made on the plexiglass at the widest width of the quadrates (head width) and from the tip of the snout to the posteriormost indication of the quadrates (head length). The plexiglass was lifted away from the head to minimize the effects of compression on head measurements. Measurements were taken along the pencil mark for total length and between appropriate marks for head dimensions using a flexible metric measuring tape (measurements recorded to the nearest millimeter).

After marking for measurements, a noose constructed from a 1.27 cm PVC pipe and 4 mm nylon rope was inserted into one end of the squeeze box through movable portals, and the tail seized and pulled out of the squeeze box. In this way the snakes were unable to strike as further examinations of the tail were completed. Tail length was measured from the cloacal scale to tail tip and subtracted from total length in order to estimate snout-vent length. Sex was determined by inserting an appropriately sized stainless steel probe into the caudal wall of the cloaca (Laszlo, 1973). Probe depth was

recorded for further analysis. Snakes were permanently marked using the method of Brown and Parker (1976; Ferner, 1979), in which ventral scales are clipped in a specified numerical pattern. Clipping was deep enough to ensure scales would not heal unscarred. Clipped areas were coated with New Skin (MedTech Laboratories, Inc., Jackson, Wyoming) to prevent infection while the incision healed.

Mass was determined by placing snakes into a cloth bag (Sup-R-Bag, FurMont Reptile Hooks, Seabrook, Texas) and weighing with a Pesola scale (weight recorded to the nearest gram; Forestry Suppliers, Inc., Jackson, Mississippi). After measurements and marking, snakes were transferred into an acrylic tube and palpated for stomach contents (see *Foraging and Feeding Ecology*). Snakes were then released at the point of capture and habitat measurements were taken (see *Habitat Analysis*).

Collection and Analysis of Data on Cottonmouths

Captured snakes.—Upon capture and recapture several variables were measured, including morphological characteristics, exposure to sun, behavior, activity, and location (Table 1; Appendix II). These measurements were considered independent for individual mark-recapture animals. Additionally, since the variables measured were generally separated by two or more days for radiotelemetered snakes, and hence likely independent of one another, radiotelemetered subjects were directly comparable to mark-recapture subjects. Scores for various categories were tallied and compared statistically by corrected chi-square analysis (Sokal and Rohlf, 1995). To evaluate the effect of temperature on behavior, the percentage of observations in each category was plotted according to the temperature at which they occurred.

Uncaptured snakes.—Fifty-three animals evaded capture during the study. Though they were not captured, behavioral data could still be obtained and analyzed. The medium from which a snake was approached (land or water) and the medium to which it escaped

TABLE 1.—Description of variables assessed during captures and relocations of cottonmouths at Back Bay National Wildlife Refuge.

Variable	Description
Snake location	
Upland	Snake position greater than 0.5 m from water source
Shoreline	Snake located less than 0.5 m from water source
Water	Snake located in water
Cover object	
Tree	Snake located under tree or shrub
Vegetation	Snake located under or in vegetation
None	Snake located in open area (including water) without cover
Sun Exposure	
Full sun	Snake positioned with at least one-half of body in full sunlight
Shade	Snake positioned with less than one-half of body in full sunlight
Full shade	Snake positioned with no exposure to sunlight
Activity	
Coiled	Snake positioned with body coiled
Extended	Snake positioned in very loose coil or in a linear position
Moving	Snake in motion when detected

TABLE 1.--Continued.

Variable	Description
Behavior	
Passive	No mouth gape or strike when approached, but includes snakes that bit tongs when grasped
Aggressive	Mouth gape and/or strike when approached and includes snakes that repeatedly bit tongs
Very aggressive	Snake struck at investigator and/or approached investigator and repeatedly struggled and bit tongs and squeeze box--these snakes kept mouth gaped during entire processing time
Action	
Flee	Snake attempted escape when approached
Approach	Snake approached investigator
Immobile	Snake made no attempt to flee or approach

(land or water) was noted for each uncaptured animal. In addition, the approach distance before fleeing was recorded.

Statistical analysis.--Morphological data (SVL, tail length, probe length, head length, head width, and body mass) were separated according to area (natural or anthropogenic marsh) and sex prior to testing. A MANOVA was used to test for area effect and sex effect after testing categories for normality using the Shapiro-Wilk test (Zar, 1996). If area effect was not significant, sexes were pooled prior to further analysis. In order to avoid the problems associated with measurements being correlated to body size, all individual measurements (with the exception of SVL) were divided by SVL prior to analysis (see Blem and Blem, 1995). These measurements were first plotted against SVL and the residuals examined for patterns that might affect results.

Growth was examined by comparing measurements of two females and six males recaptured approximately one year after their initial captures. Mean growth and associated error are reported for both sexes; however, further statistical analysis cannot be justified given the small sample sizes, though general comments can be drawn.

Categorical analysis was conducted on location (upland, water, or shoreline), cover (tree, vegetation, or none), sun exposure (full sun, shade, or full shade), activity (extended, moving, or coiled), action (stand ground, flee, or approach), and behavior (aggressive, very aggressive, or passive). Separate chi-square statistics were calculated for each group (males in natural marsh, females in natural marsh, males in anthropogenic marsh, females in anthropogenic marsh, and radiotelemetered snakes) using Yates' continuity correction (Sokal and Rohlf, 1995). For comparisons across groups, expected values were calculated based on sample-size dependency because sample size was not the same for all groups. Alpha levels were set at 0.05 for all tests; however, in order to protect the error rate for individual comparisons, a Bonferonni correction (Sokal and Rohlf, 1995) was used. That is, the alpha level was divided by the intended number of tests before comparisons with critical values were made.

Contingency table analysis was used on the uncaptured snake data in order to test for independence of "approach from" and "flee to" variables. A two-sample t-test with unequal variances (following F_{\max} statistical comparisons) was used to test for differences in approach distance between animals in the natural and anthropogenic marsh systems.

Inasmuch as error is difficult to measure from field measurements of size, the five radiotelemetric subjects were measured in both the field and laboratory in order to verify the accuracy and precision of the procedure. Mean differences and associated errors are reported.

Habitat Analysis

Unless noted otherwise in this section, all statistical analyses were conducted using the Statistical Analysis System (SAS; Cary, North Carolina). For completeness and to facilitate discussion, procedures (PROC) are given in the appropriate sections.

Data collection.--Habitat data were collected for each snake captured during the study and upon the relocation of each radiotelemetered animal. In addition, 100 random sites in the natural marsh and 100 random sites in the anthropogenic marsh were sampled during the final field season. Eleven habitat variables were selected to describe each location. The variables chosen for analysis consisted of vegetative structural characters as well as distance to water, presumably an important factor for the cottonmouth (Table 2). In addition to structural elements, notes on species composition were also made (Appendix I). Variables were selected to facilitate comparison with previous analyses of pitviper habitat (Reinert 1984a,b; Reinert 1992; Petersen, 1995).

Data were obtained by centering a 1 m² quadrat on each snake location or random site. In instances where a 1 m² quadrat was not available, snake tongs marked with a 1 m scale were used to mark an approximate 1 m² area. Random points were selected by using

TABLE 2.—Habitat variables measured at random sites, capture sites, and sites occupied by radio-tracked cottonmouths at Back Bay National Wildlife Refuge.

Habitat variable	Variable abbreviation	Sampling method
Distance to water	DW	Distance (m) from center of 1 m ² quadrat
DBH of overstory tree	DBO	Diameter at breast height (cm) of nearest overstory tree (≥ 7.0 cm) not inside of 1 m ² quadrat
Distance to overstory tree	DOT	Distance (m) to nearest overstory tree (≥ 7.0 cm dbh) not inside of 1 m ² quadrat
DBH of understory tree	DBU	Diameter at breast height (cm) of nearest understory tree (< 7.0 cm) not inside of 1 m ² quadrat
Distance to understory tree	DUT	Distance (m) to nearest understory tree (< 7.0 cm dbh) not inside of 1 m ² quadrat
Percent canopy closure	CAN	Canopy closure (%) directly above 1 m ² quadrat
Percent leaf cover	LEAF	Leaf cover (%) within a 1 m ² quadrat
Percent debris cover	DEB	Debris cover (%; dead vegetation, logs, debris washed ashore from water, etc.) within a 1 m ² quadrat
Percent vegetation cover	VEG	Vegetation cover (%) within a 1 m ² quadrat
Vegetation density	DENS	Density (stems/m ²) within a 1 m ² quadrat
Height of dominant vegetation	HT	Height (m) of dominant vegetation within a 1 m ² quadrat

a uniform random numbers table (Thompson, 1992 : 14). The first three digits of the chosen random number were used as a compass direction from a starting location and the second three numbers were used as the number of paces from a starting location. Several independent starting points were used so that the entire study area was represented in the natural marsh and each pool was represented in the anthropogenic marsh. The 1 m² quadrat for a random location was placed directly in front of the investigator in the same compass direction traversed.

Variables were measured using techniques similar to those of Reinert (1984a,b) and Petersen (1995), although different techniques were used for several measurements. Diameter at breast height (dbh) for both understory and overstory trees was measured with a dbh tape graduated in centimeters (Forestry Suppliers, Inc. Jackson, Mississippi). In instances where the popularly accepted dbh measuring height of 1.37 m (4.5 ft; Higgins et al. 1994) was not possible (i.e., when a tree had a divided bole), the dbh of the largest bole was used. Distances to understory and overstory trees and vegetation heights were measured with a metric tape. Leaf cover, debris cover, and vegetation cover were estimated visually. Canopy closure was estimated using a 100 cm² mirror (standard military issue, Boy Scouts of America) marked with a 10 X 10 grid (1 cm²/grid). The mirror was held in the center of the 1 m² quadrat at waist height, and closure was estimated by counting the number of grid elements where canopy could be seen. Vegetation density was either directly counted (when vegetation was nonuniformly distributed in the quadrat) or estimated by counting stems in the lower right one quarter of the quadrat and multiplying by four (when vegetation was uniformly distributed in the quadrat).

Several classes of sites were used for initial habitat analysis. Random sites, known snake collection sites, and location sites for radiotelemetered animals were separated before comparisons. Male and female snakes were further grouped according to location (either natural marsh or anthropogenic marsh; Table 3). Given the difficulties associated

TABLE 3.—Categories of random and *Agkistrodon p. piscivorus* sites used in habitat modelling comparisons. See text for explanation of sample sizes and description of sampling protocol for each category.

Sampling category	Category abbreviation	<i>n</i>
Random natural marsh sites	RN	100
Random anthropogenic marsh sites	RA	100
Natural marsh males	NM	43
Anthropogenic marsh males	AM	17
Natural marsh females	NF	23
Anthropogenic marsh females	AF	11
Radiotelemetry subject 1 (natural marsh male)	AP-1	29
Radiotelemetry subject 2 (natural marsh male)	AP-2	56
Radiotelemetry subject 3 (natural marsh female)	AP-3	59
Radiotelemetry subject 4 (anthropogenic marsh female)	AP-4	22
Radiotelemetry subject 5 (anthropogenic marsh male)	AP-5	20

with serial correlation of movement data (Swihart and Slade, 1985a,b, 1986, 1997; Swihart et al., 1988; Reinert, 1984a; b), only habitat variables collected from different relocations of individual animals were used in habitat analyses. That is, if an animal was found in the same location (movements < 1.0 m from previous location) for several days, the variables associated with that location were used only once in the analysis. Habitat characteristics of hibernacula also were not used for comparative purposes to avoid autocorrelation.

Use-intensity classification.—Use-intensity classifications were based upon a plot of snake locations on the map of BBNWR. The study area was divided into square grid cells of 156.25 m² (12.5 m on each side). The distance from the center of a grid cell to any side was within the range of distances that individual snakes moved in a day, based on radiotelemetric data. Therefore, a given snake could be in a different grid square on any given day. Habitat components for each grid cell represented a mean of the locations found within them. With these criteria, 79 individual grid cells comprised the sample. For use-intensity classification, BBNWR was not divided into natural and anthropogenic marshes, but rather was treated as one study area (see DISCUSSION).

Plotting the percentage of the telemetry points located in specific grid cells and summing over all snakes allowed for use-intensity classes to be assigned. The number of categories varies from study to study, and delineating them relies upon graphical patterns or, in their absence, on biological intuition concerning the species under study (North and Reynolds, 1996). Three categories were used in this study: low use, middle use, and high use. They were delineated by obvious patterns in the graph (see RESULTS) and modeled as described below.

Multivariate regression and analysis of variance.—Initial analyses of the data were performed to evaluate normality of individual habitat variables (PROC UNIVARIATE). As is common with habitat variables, the assumption of normality is rarely met (Reinert, 1984a; Noon, 1986; Cross, unpublished), due largely to the nature of the variables in

question. Leaf litter cover, for example, is usually either very high (near 100% coverage) or very low (0-5% coverage), with very few intermediate points, and the same is true for many other variables. This often gives rise to skewed or platykurtic distributions, in which there are more measurements in the tails than would be expected by chance (Sokal and Rohlf, 1995; Zar, 1996). Many data transformations are available to resolve these problems, and they often lead to biologically identical results (Reinert, 1984a). However, extremely platykurtic distributions often cannot adequately be transformed into a mesokurtic distribution, and thus other methodologies must be examined.

If the data are moderately evenly distributed about the median (Bain and Engelhardt, 1987; Hogg and Craig, 1995), then nonparametric procedures can be used. Therefore, PROC RANK was used to rank the habitat measurements, and was followed by PROC GLM to produce a general linear model based on these rankings. This is equivalent in SAS language to using PROC NPAR1WAY, but is a more straightforward programming task. To test whether multidimensional means (habitat centroids; Cooley and Lohnes, 1971; Reinert, 1984a) differed between sites, a multivariate analysis of variance (MANOVA) was used on the ranked data. Only main effects were used in the analysis, after an initial examination of interaction and power terms revealed that they were not significant.

To examine differences between sites in specific variables, a multiple comparison procedure was used (*SAS User's Guide, Vol. 2*; Sokal and Rohlf, 1995). Tukey's Studentized Range (HSD) test, which controls type I experimentwise error (*SAS User's Guide, Vol. 2*), was chosen for the analysis because it is generally robust to unequal sample sizes (Sokal and Rohlf, 1995).

A canonical analysis of the sum of squares and cross-product matrices and the error matrix was used in lieu of the default MANOVA printout of characteristic roots and vectors (*SAS User's Guide, Vol. 2*). This analysis was used to find habitat variables that were most important in discriminating between different sites. This analysis can be

performed using a discriminant analysis in SAS (PROC CANDISC). However, that analysis presumes that the data are multivariate normal with equal variance-covariance matrices across groups (*SAS User's Guide, Vol. 2*; Khatree and Naik, in prep.), an assumption not met by the data. Therefore, a separate discriminant analysis was performed using nonparametric techniques.

When assumptions cannot be made about a distribution, or when normality is not assumed, a nonparametric discriminant procedure can be used in PROC DISCRIM (*SAS User's Guide, Vol. 2*). Therefore, a normal kernel estimator with a smoothing parameter of 0.2, estimated from the data (*SAS User's Guide, Vol. 2*), was used. Essentially, this method uses a computer-intensive approach to estimate group-specific densities without the constraints of normality or equal variances (*SAS User's Guide, Vol. 2*; Hocking, 1996). This procedure allows the most important discriminatory variables to be identified and also produces an error-rate classification using a cross-validation jackknifing technique (*SAS User's Guide, Vol. 2*).

Polytomous logistic regression.--The methods described above to compare use sites (sites where an animal was found) and non-use sites (randomly selected sites where it is assumed the animal is absent) are common in the literature (Shugart, 1981; Reinert 1984a,b; 1988; Petersen, 1995) and are discussed at length in several studies (Johnson, 1980; Marcum and Loftsgaarden, 1980; Fagen 1988; Thomas and Taylor, 1990). These techniques were used in the present study principally to facilitate comparisons with other studies of this type. Also, they were used to facilitate comparisons with a different modeling technique, polytomous logistic regression (PLR). PLR models the probability that a site belongs to a particular use-intensity category as a function of the microhabitat measures at a site, while retaining the information in the ordinal ranking of the dependent variables (Anderson, 1984; McCullagh and Nelder, 1989; North and Reynolds, 1996). PLR is easily performed using PROC LOGISTIC. This technique has been used to model use-intensity classes of spotted owls (North and Reynolds, 1996), and has previously been

investigated as a technique for modeling habitat use by *Agkistrodon contortrix* by the investigator (Cross, unpublished).

Following the terminology of Hosmer and Lemeshow (1989) and using slight modifications of the PLR modeling technique presented in full by North and Reynolds (1996) :

Let $\mathbf{X} = (x_1, x_2, \dots, x_n)$

= the vector of microhabitat measurements taken in a given grid cell, and

$\pi_i(\mathbf{X})$ = the probability that a site with microhabitat vector \mathbf{X} belongs to use category i ($i = 1, 2, \dots, k$), where higher i equates higher use.
(Note that $\sum_{i=1}^k \pi_i(\mathbf{x}) = 1$ and $\pi_k(\mathbf{x}) = 1 - \sum_{i=1}^{k-1} \pi_i$)

The cumulative probability that a site with vector \mathbf{X} belongs to use category i is given by:

$$F_i(\mathbf{X}) = \pi_1(\mathbf{X}) + \pi_2(\mathbf{X}) + \dots + \pi_i(\mathbf{X}),$$

for $i = 1, 2, \dots, k-1$, and further

$$F_k(\mathbf{X}) = 1 - F_{k-1}(\mathbf{X}) = \pi_k(\mathbf{x}) = 1 - \sum_{i=1}^{k-1} \pi_i$$

For modeling purposes, a link function (McCullagh and Nelder, 1983), also known as the log-odds ratio (Hocking, 1996), is necessary to ensure that a function of the dependent variables is a linear function of the independent variables (Hosmer and Lemeshow, 1989). The link function for logistic regression is the logit transformation (Hosmer and Lemeshow, 1989) and is defined as:

$$L_i(\mathbf{X}) = \text{logit}(F_i(\mathbf{X})) = \ln[F_i(\mathbf{X}) / (1 - F_i(\mathbf{X}))].$$

PLR models the logit function as a linear function of the microhabitat variables and makes the assumption of proportional odds (Hosmer and Lemeshow, 1989; North and Reynolds, 1996). That is, the functions differ only by their associated α (the intercept) and not by their β 's (the slopes). Hence,

$$L_i(\mathbf{X}, \alpha_i, \beta) = \alpha_i + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n$$

for $i = 1, 2, \dots, k-1$, and

$$L_k(\mathbf{X}, \alpha_i, \beta) = -(\alpha_{k-1} + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n)$$

for $i = k$.

The parameters are estimated by the method of maximum likelihood (Hosmer and Lemeshow, 1989).

The estimated probability that a given site belongs to a particular use category can be calculated from the estimated logit functions:

$$\hat{F}_i(\mathbf{X}) = 1 / [1 + \exp(-L_i(\mathbf{X}, \hat{\alpha}_i, \hat{\beta}))]$$

for $i = 1, 2, \dots, k$,

which are:

$$\hat{\pi}_1(\mathbf{X}) = \hat{F}_1(\mathbf{X}),$$

$$\hat{\pi}_i(\mathbf{X}) = \hat{F}_i(\mathbf{X}) - \hat{F}_{i-1}(\mathbf{X}),$$

for $i = 2, 3, \dots, k-1$, and finally

$$\hat{\pi}_k(\mathbf{X}) = \hat{F}_k(\mathbf{X}).$$

The fit of the model can be assessed by calculating the classification errors of the original model. A jackknife procedure is recommended because error probabilities may be biased if calculated from the original data (*SAS User's Guide, Vol. 2*; North and Reynolds, 1996). However, this would require generating 79 different models in SAS. Since no algorithm is currently available for generating classification errors of polytomous variables, a slight positive bias exists in the reported classification errors.

Estimation of Population Size

Estimates of population size were calculated using slight modifications of Schnabel's multiple census method (1938; hereafter called Schnabel Index; Seber, 1982). The Schnabel Index is a multiple mark-recapture estimation technique useful for estimating closed populations. This technique is an extension of the single mark-recapture estimator obtained by the Lincoln-Petersen method (see Seber, 1982).

As with any closed population model, the primary assumption is that there are no animals entering (via births or immigration) or leaving (via deaths or emigration) the population during the sampling period. Several statistical tests for population closure can be found in the literature (Burnham and Overton, 1978; Robson and Flick, 1965; Otis et al., 1978). However, Otis et al. (1978) suggest that these tests are weak and that the best way to ensure closure is to design your study in such a way that the assumption of closure is met as closely as possible (see also Seber, 1982), as described below.

The bulk of the mark-recapture data for this study came from captures during the months of May-October, 1996-1997, with some captures occurring outside these periods. Only three dead snakes (unmarked) were found during the duration of the study, hence deaths were assumed to be negligible. The few juveniles entering the population

from late August through September were marked and released, but were not used to estimate population size; therefore, births were considered to be zero (no juveniles were recaptured). A few cottonmouths were observed in the open water of Back Bay during the study while on boating excursions to Long Island to search for snakes. Given the sparse cottonmouth population on Long Island (Cross, unpublished data) and few sightings, migration during the study period was assumed to be of little consequence. Since no marked snakes (either scale-clipped or radiotelemetered) were found to have moved between natural and anthropogenic marshes, each of these areas was assumed to be closed relative to the other. Finally, animals marked and released in late 1995 and in 1996 that were recaptured in 1997 were not included in population estimates in order to insure independent estimates across years.

A second major assumption of the proposed technique is that the probability of capture is equal among members of the population ("equal catchability;" Eberhardt, 1969; Krebs, 1989; Seber, 1982). This can be tested using the zero-truncated Poisson test of equal-catchability (Caughley, 1977; Krebs, 1989). This technique uses the frequency distribution of numbers of animals caught various times during the survey and then compares these observed frequencies to expected frequencies obtained from a zero-truncated Poisson distribution using a chi-square goodness of fit test (Krebs, 1989; Seber, 1982). This technique was used in this investigation.

Estimating the number of snakes.—Separate estimates of population numbers were obtained for 1996 and 1997 for both the natural and anthropogenic marsh systems. The marsh systems were divided into several transects for sampling (see Introduction) and were sampled five to six days per week. Since both systems consisted of several kilometers of sampling transects, not all transects could be sampled each day. Therefore, particular transects in both areas were randomly sampled on each sampling occasion in such a way that transects in each marsh system were sampled in their entirety every week.

Sampling occasions were taken as the summation of the individual transects sampled over a week's time.

Using slight modifications of Kreb's (1989) and Seber's (1982) notation, let

N = population size,

s = number of sampling occasions = sum of all transects samples over each of several days (d) of the week (see text)

C_i = number of animals captured on the i^{th} occasion ($i = 1, 2, \dots, s$),

R_i = number of marked (recaptured) animals in C_i

M_i = number of marked individuals in the population just before the i^{th} sample is taken
 $= \sum_{j=1}^{i-1} (C_j - R_j)$ ($i = 1, 2, \dots, s+1$), where M_{s+1} is defined as the total number of different individuals captured throughout the entire sampling period.

Schnabel (1938; Bailey 1951, 1952) treated each M_i as a fixed parameter and used the binomial approximation:

$$f(R_2, \dots, R_s | C_i, M_i) = \prod_{i=2}^s \binom{C_i}{R_i} \left(\frac{M_i}{N} \right)^{R_i} \left(1 - \frac{M_i}{N} \right)^{C_i - R_i}.$$

Using maximum-likelihood theory (Edwards, 1992), the estimate of population size was approximated by (Krebs, 1989; Seber, 1982):

$$\hat{N} = \frac{\left(\sum_{i=2}^s C_i M_i \right)}{\sum_{i=2}^s R_i}$$

with variance approximated by (Krebs, 1989):

$$\text{Var}\left(\frac{1}{\hat{N}}\right) = \frac{\sum_{i=2}^s R_i}{\left(\sum_{i=2}^s C_i M_i\right)^2}.$$

This estimate of population size is simply a modified Lincoln-Petersen estimate over a series of s , rather than two, capture occasions (Seber, 1982). A confidence interval for the estimate of population size can be found using asymptotic normal theory if $R_i > 50$ (Seber, 1982). However, in most mark-recapture studies of snakes, as well as in the present study, the number of recaptures is much less than 50. Therefore, Seber (1982), following the work of Chapman (1951), suggests using the Poisson distribution, since $R_i \sim \text{POI}(C_i M_i / N)$. This often results in very wide confidence intervals about the estimate, as seen in the Results, below.

An additional result of using the Schnabel Index was derived by Chapman and Overton (1966) and is particularly useful in the present study. If a Schnabel Index is calculated for two populations, then the population estimates can be compared statistically by converting the estimates to a normal z deviate with a continuity correction and then comparing the result to a statistical table. If N_n and N_a are the estimates of snake numbers in the natural and anthropogenic marsh systems, respectively, R_n and R_a are the total number of recaptures in both systems, Q_n and Q_a are the sums of the products of C_i and M_i from above for each population, and $p = Q_n / Q_a$, then we can test the null hypothesis $H_0: N_n = N_a$ against the alternative hypothesis $H_a: N_n \neq N_a$ using the following equation:

$$z = \frac{|R_n - (R_n + R_a) \times p| - \frac{1}{2}}{\sqrt{(R_n + R_a) \times p \times (1 - p)}}.$$

Estimating the density of snakes.—Estimating density directly from population point estimates is not always a straightforward task because the area sampled and the area used to determine density generally are not identical. Thus, estimated density may be biased

(Anderson et al., 1983; Dice, 1938; White et al., 1982). If it is assumed that the area sampled includes the entire area of interest, then the finite population estimate of density (Buckland et al., 1993; Cochran, 1977), where \hat{N} = the population point estimate, and a = survey area, is given by:

$$\hat{D}_a = \frac{\hat{N}}{a}.$$

Estimating linear density (King, 1986; Parker and Plummer, 1987), however, may be more appropriate considering that the area surveyed in this study concentrated on the shoreline habitat of natural and anthropogenic marshes. Assuming that the density of snakes is constant along the lengths of shoreline sampled, and letting l = the linear extent of shoreline surveyed (natural marsh = 6340 m; anthropogenic marsh = 9860 m), density can be estimated by the following equation:

$$\hat{D}_l = \frac{\hat{N}}{l}$$

Both approaches were used in this study.

Trophic Ecology and Behavior

Gut contents were obtained opportunistically from several snakes ($n = 56$) in both marsh systems. An attempt was made to balance sampling, as much as possible, between the two areas and between sexes; however, balanced sampling could not be done in both areas given the difficulty in obtaining gut contents of snakes. In addition, three snakes found dead on the Refuge were dissected to obtain gut contents. After cottonmouths were captured and processed according to the protocols of the mark-recapture study, snakes were secured by placing their head and approximately 10 cm of their neck into an

appropriately sized clear acrylic tube (see Reinert, 1992). Stomach contents were gently palpated by finger pressure to within a few centimeters of the head (Fitch, 1987), after which the snake was placed into a squeeze box where the food was regurgitated by the animal. Items were collected, bagged, sealed, labeled for future identification, and frozen. Contents were later weighed, measured, and identified by the principal investigator.

In order to obtain information on prey availability, both marsh systems were sampled for potential prey items. Information on prey fishes and small mammals were gathered from various survey studies performed at BBNWR by private investigators and USFWS staff. Information on potential waterfowl prey items was obtained from weekly surveys by the principal investigator and USFWS biologists. Amphibian prey items were identified by observations during the course of the study. Dip-net sampling of ditches during the nighttime hours was used to estimate amphibian density.

Radiotelemetry

Implantation of radiotransmitters.--Five adult snakes (two males and one female from the natural marsh and one male and one female from the anthropogenic marsh) were implanted with temperature-sensitive radiotransmitters (Model SM1; AVM Instrument Company, Ltd., Livermore, California) during the course of this investigation.

Transmitters ranged from 8-10.5 g, a mass small enough to ensure that transmitter weight was much less than 5% of the implanted snake's body mass (range = .8% - 2.7%; Reinert, 1992). The transmitters were calibrated by submersion in seven water baths ranging from 0.4-47.8 C before implantation to derive a relationship between pulse interval and temperature. A linear relationship was established for one radio (an older model with a mercury oxide battery) and exponential relationships were found for five radios (newer models with silver oxide batteries).

Snakes were captured and brought into the laboratory for surgical implantation of radiotransmitters, following the method of Reinert and Cundall (1982; Reinert, 1992). Transmitters were coated with a solution of beeswax and paraffin (1:1 by mass) before implantation. Snakes were anesthetized using an acrylic chamber into which isoflourane anesthetic (Aerrane) had been placed within a perforated bottle. After the snakes were fully anesthetized, they were removed and measured. Following measurements, snakes were placed onto a surgical drape, lightly strapped to a board for safety, and maintained under anesthesia by means of a mask that contained isoflourane (Reinert and Cundall, 1982). Transmitters were implanted into the pleuroperitoneal cavity by making a small incision between the first and second scale rows approximately 75% of the SVL from the snout. Each radiotransmitter was equipped with a whip antenna, which was placed subcutaneously and anterior to the radiotransmitter. Incisions were closed using 3X0 Prolene sutures and coated with a surgical adhesive (New Skin).

Tracking and monitoring.—Snakes were monitored for various lengths of time (see Results) from early fall, 1996 through late spring, 1998. Tracking of snakes generally was performed at least once every two days during the spring, summer, and autumn, and at least once every three days during hibernation. Tracking usually took place during the morning or early afternoon hours. A Wildlife Materials receiver (model TRX-1000S; Wildlife Materials, Inc., Carbondale, Illinois) equipped with a collapsible three-element Yagi antenna (AVM Instrument Company, Ltd., Livermore, California) was used to track snakes. Maximum range was approximately 600 m in open marsh and considerably less elsewhere.

Latitude and longitude positions were obtained for relocated snakes using a global positioning system (GPS) receiver (Trailblazer XL; Magellan Systems Corp., San Dimas, California). Additionally, distances and direction to known, mapped locations were taken from relocation sites to ensure accurate mapping. Pulse interval was obtained for each relocation (see Temperature data, below). Habitat measurements were also taken at each

site at the time of snake relocation (see Habitat, above). Locations were mapped according to GPS and triangulation data using a metric ruler and 360° protractor.

Movements and activity range areas.—The total distance moved was determined by summing the linear distances between successive relocation sites. Mean distance moved per day and mean distance per movement were calculated by dividing the total distance moved per day by the number of days tracked and the total number of movements a snake made, respectively. Range length was defined as the linear distance between the two most distant locations (Reinert, 1992; Petersen, 1995). Activity ranges were found by entering the relocation data as Cartesian coordinates into program McPAAL (Michael Stuwe, Conservation and Research Center, National Zoological Park, Washington, D. C.). Areas of use were determined by both the geometry of the minimum convex polygon constructed by connecting the outermost vertices of the polygon constructed from the relocation data and the area enclosed by the 95% isopleth using the harmonic mean method (White and Garrott, 1990). Activity ranges for 17 recaptured snakes provided ancillary data for comparisons with the radiotelemetric subjects. Areas for these snakes were found by plotting and connecting relocation points, and then applying an appropriate geometric formula (e.g., $A = 0.5(\text{base})(\text{height})$ for a triangle). There were four females and 13 males with adequate data for these calculations.

Movement patterns were determined by calculating the biweekly mean movement per day of each individual during the active season. These means were calculated by summing the total distance moved over a two week interval, then dividing by 14 days (see Petersen, 1995). Data were plotted but not compared statistically due to limited sample sizes.

Temperature data.—Air, surface, and soil (10 cm depth) temperatures were taken at each relocation site using a digital Electro-Therm thermometer (model SH66A; Cooper Instrument Corp.). Body temperatures were found by recording the pulse interval of the

snake and then comparing it to the standard curves of pulse interval versus temperature for each radio.

Mean body, air, surface, and soil temperatures were calculated for each snake during both the active season and in hibernation. Correlations of body temperature with environmental temperatures were also calculated for both the active season and hibernation. Grand means, determined by weighting individual means by sample size (weighted means), were calculated for all variables.

To elucidate the possible temperature cues used by snakes to enter hibernacula in late autumn (ingress) and to exit hibernacula in spring (egress), weekly mean temperatures (air, surface, and soil) were calculated for eight weeks. Means for the two weeks prior to and after ingress and for the two weeks prior to and after egress were plotted. Ingress and egress dates and snake body, air, surface, and soil temperatures were plotted simultaneously for comparison.

Management of Cottonmouths

Visitors to BBNWR are encouraged to leave a note in the "Animal Sighting Log" before leaving the Refuge. Many visitors see snakes along public access trails and make notes of their observations. Also, hunters have access to the Refuge for one week each October. A sighting log was made available during the hunt week of 1997, and several hunters left notes on snake sightings. In both cases (visitors and hunters), plots were made to show snake sightings at BBNWR. Given the common occurrence and sightings of cottonmouths, management implications were developed for cottonmouths at the Refuge.

RESULTS

Ecological Analyses

Morphological measurements.—The largest snakes captured were males, but much overlap was seen in SVL. Tail length was greatest in males also, but a large area of overlap was evident when not corrected by SVL. Probe length (i.e., inverted length of the hemipenis) was large in males compared to females. Head length, head width, and body mass all showed large overlap between males and females.

Descriptive statistics for morphological measurements for each group of animals (area and sex) and overall (pooled) were quite similar, with the obvious exception of probe length (Table 4). MANOVA results for area effect showed that differences between natural and anthropogenic marsh systems were all statistically insignificant, as was the test for overall area effect ($P > 0.05$; Table 5). Therefore, snakes from the two habitat types were grouped prior to testing for sexual differences. Overall effect of sex was significant ($P \leq 0.0001$), with both relative (i.e. SVL-corrected) tail length and probe length statistically significant ($P = 0.0444$ and $P \leq 0.0001$, respectively; Table 6).

Growth and difference measurements.—There were few recaptures over time, making growth difficult to assess in the present study. However, two females and six males were recaptured approximately one year after initial capture, allowing annual growth rates to be estimated. Males showed greater growth in all morphological categories except tail length and mass (Table 7).

Given that field measurements of snakes have associated error, making growth assessment difficult if the error is great enough, all radiotelemetry subjects were measured in the field using the same technique as for mark-recapture specimens. After being brought to the laboratory, animals were remeasured using a method assumed to be more accurate (measurements were taken directly on anesthetized snakes). Differences in field

TABLE 4.--Morphological measurements for cottonmouths at Back Bay National Wildlife Refuge. Snout-vent length (SVL) is given, as are measurement/SVL ratios. Measurements are presented as \bar{x} (n , SE).

	All groups	NM	AM	NF	AF
Snout-vent length (SVL)	650.19 (94, 17.501)	677.99 (45, 30.801)	625.94 (17, 40.996)	623.62 (20, 14.628)	624.58 (12, 38.409)
Tail length/SVL	0.19 (94, 0.020)	0.19 (45, 0.012)	0.20 (17, 0.003)	0.16 (20, 0.006)	0.18 (12, 0.005)
Probe length/SVL	0.06 (89, 0.006)	0.08 (43, 0.003)	0.08 (17, 0.005)	0.02 (17, 0.003)	0.01 (12, 0.001)
Head length/SVL	0.06 (88, 0.006)	0.06 (43, 0.002)	0.06 (17, 0.002)	0.06 (17, 0.001)	0.07 (11, 0.001)
Head width/SVL	0.05 (85, 0.005)	0.05 (40, 0.003)	0.05 (17, 0.005)	0.05 (17, 0.003)	0.05 (11, 0.001)
Mass/SVL	0.67 (67, 0.072)	0.66 (29, 0.048)	0.70 (15, 0.055)	0.64 (14, 0.054)	0.65 (9, 0.059)

TABLE 5.--Results of MANOVA testing for differences in morphological characteristics of snake populations between natural and anthropogenic marsh systems at Back Bay National Wildlife Refuge. Morphological characters were divided by snout-vent length prior to analysis (see text). Wilks' Lambda for overall area effect is given.

Dependent Variable	Numerator df	Denominator df	F	P
Snout-vent length (SVL)	1	64	1.330	0.2523
Tail length / SVL	1	64	0.001	0.9496
Probe length / SVL	1	64	3.890	0.0529
Head length / SVL	1	64	0.780	0.3801
Head width / SVL	1	64	0.530	0.4691
Mass / SVL	1	64	0.280	0.6016
Wilks' Lambda	6	59	0.998	0.4353

TABLE 6.--Results of MANOVA testing for differences in morphological characteristics of snake populations between sexes at Back Bay National Wildlife Refuge. Natural and anthropogenic populations were pooled prior to analysis since no area effect was found (see text). Morphological characters were divided by snout-vent length prior to analysis (see text). Wilk's Lambda for overall area effect is given.

Dependent Variable	Numerator df	Denominator df	F	P
Snout-vent length (SVL)	1	92	1.160	0.2844
Tail length / SVL	1	92	4.160	0.0444
Probe length / SVL	1	87	280.900	0.0001
Head length / SVL	1	86	0.040	0.8434
Head width / SVL	1	83	0.070	0.7991
Mass / SVL	1	65	0.360	0.5526
Wilks' Lambda	6	60	54.754	0.0001

and laboratory measurements were less than 1 cm in all morphological categories (Table 7). Loss of body mass for snakes brought into the laboratory was fairly dramatic (Table 7), but not uncommon compared to other taxa (A. H. Savitzky, personal communication).

Location—More snakes were found at upland sites (≥ 0.5 m from water source) than in either water or shoreline locations, with radiotelemetry specimens generally spending the greatest amount of their time away from water. However, males in the anthropogenic habitat had the higher percentage of captures in the water (Table 8; Fig. 2).

Cover object—Most snakes found used vegetation as a source of cover, with radiotelemetry subjects and males in the anthropogenic marsh using vegetation most often. Several individuals, notably males and females in the natural marsh and females in the anthropogenic marsh, were found in the absence of cover (Table 9; Fig. 3).

Sun exposure—The majority of captures and relocations of animals showed full sun exposure, suggesting high basking behavior. The radiotelemetry male in the anthropogenic marsh (AP-5) was the exception, with the majority of his relocations in full shade (Table 10; Fig. 4). The majority of snakes were found in full sun regardless of temperature (Fig. 5-Fig. 8); however, a large percentage of radiotelemetry female relocations was in shade regardless of temperature (Fig. 8).

Activity—Most snakes located in this study were either lying extended or coiled; few were moving. Chi-square significance between activity categories was only found in radiotelemetry animals AP-1 through AP-4, with AP-1 through AP-3 most often extended, and AP-4 most often coiled. A male in the natural marsh (AP-2) was most often extended, whereas the female in the natural marsh (AP-3) was most often coiled (Table 11; Fig. 9). Although most snakes were motionless at all temperatures, movement was most common at temperatures > 18 C (Fig. 5-Fig. 8).

Defensive movement.—Nearly all snakes did not move when located, with few fleeing or approaching the investigator. Chi-square tests indicated that the "no movement" category was observed much more often than expected in all categories except

TABLE 7.—Difference measurements of cottonmouths at Back Bay National Wildlife Refuge. Growth (in mm) for two females and six males (natural and anthropogenic marsh systems are presented together; see text) separated by one year between initial capture and recapture are shown. Additionally, field versus laboratory measurements are given for five radiotelemetry snakes. Measurements are presented \bar{x} (SE).

	Females	Males	Radiotelemetry snakes
Snout-vent length	26.50 (6.501)	43.83 (11.633)	+6.00 (0.837)
Tail length	14.50 (4.501)	14.17 (3.651)	+2.51 (1.022)
Probe length	1.70 (0.000)	5.50 (1.886)	0.00 (1.000)
Head length	0.00 (0.000)	5.67 (1.861)	+0.90 (0.900)
Head width	2.00 (0.000)	5.60 (1.592)	-0.90 (1.646)
Mass	70.00 (5.000)	50.00 (42.817)	-59.68 (12.148)

TABLE 8.--Location for cottonmouths at Back Bay National Wildlife Refuge. Capture locations for mark-recapture snakes (NM-AF) and resight locations for radiotelemetry snakes (AP-1-AP-5) were placed into three categories and compared using chi-square tests with Yates' continuity correction (Sokal and Rohlf, 1995). Appropriate alpha-levels and degrees of freedom (total chi-square: $\alpha = 0.05$, $df = 2$; partial chi-squares $\alpha = 0.01$, $df = 1$) are described in the text. Asterisks indicate statistical significance.

	NM	AM	NF	AF	AP-1	AP-2	AP-3	AP-4	AP-5
Upland	19	5	17	3	19	53	78	12	11
Water	23	13	8	6	4	1	1	4	5
Shoreline	15	0	1	3	3	6	2	6	11
Total chi-square	1.30	12.13*	13.00*	0.69	16.24*	79.04*	140.77*	3.56	1.86
Upland vs. Water	0.21	7.08*	2.56	0.44	8.52*	48.17*	73.11*	3.06	1.56
Upland vs. Shoreline	0.26	3.2	12.5*	0.17	10.23*	35.86*	70.31*	1.39	0.05
Water vs. Shoreline	1.29	11.08*	4.00	0.44	0.00	2.29	0.00	0.10	1.56

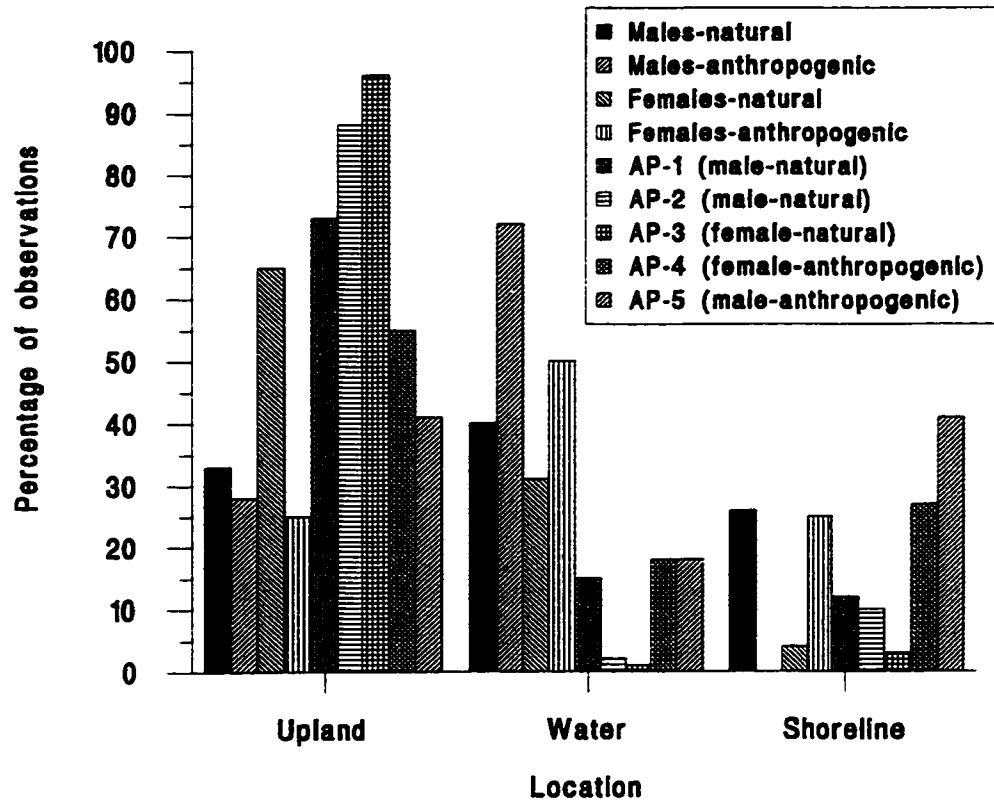


FIG. 2.--Location (as percentage of observations) for cottonmouths at Back Bay National Wildlife Refuge.

TABLE 9.--Cover object data for cottonmouths at Back Bay National Wildlife Refuge. Cover type for mark-recapture snakes (NM-AF) and resight data for radiotelemetry snakes (AP-1-AP-5) were placed into three categories and compared using chi-square tests with Yates' continuity correction (Sokal and Rohlf, 1995). Appropriate alpha-levels and degrees of freedom (total chi-square: $\alpha = 0.05$, $df = 2$; partial chi-squares $\alpha = 0.01$, $df = 1$) are described in the text. Asterisks indicate statistical significance.

	NM	AM	NF	AF	AP-1	AP-2	AP-3	AP-4	AP-5
Tree	12	1	4	1	6	1	2	0	2
Vegetation	15	16	6	2	16	56	56	21	13
None	24	1	16	9	4	4	6	1	9
Total chi-square	3.81	21.79*	7.93*	7.19*	7.93*	90.59*	81.66*	34.65*	6.34*
Tree vs. Vegetation	0.15	0.05	0.10	0.00	3.68*	51.16*	48.43*	19.05*	6.67*
Tree vs. None	3.36	11.53*	6.05	4.90	0.10	0.80	1.13	0.00	3.27
Vegetation vs. None	1.64	11.52*	3.68	3.27	6.05	43.35*	38.73*	16.41*	0.41

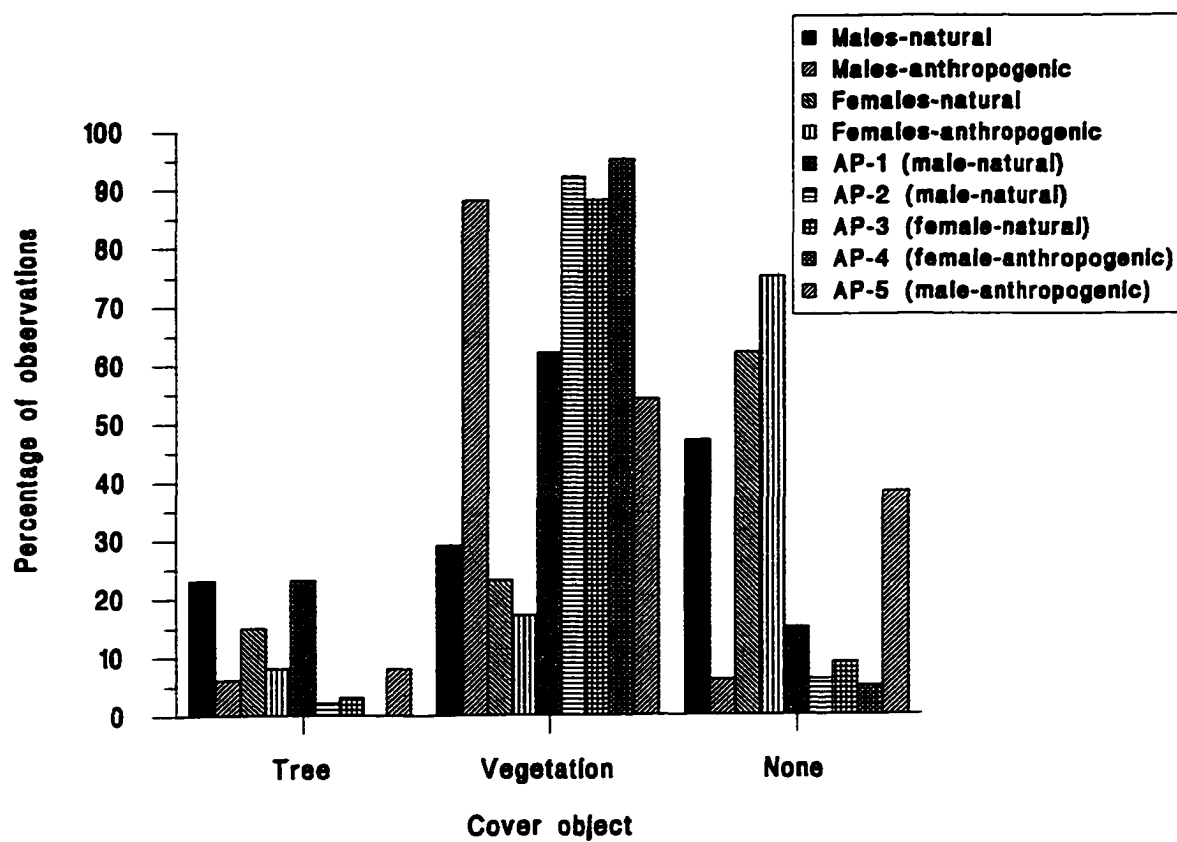


FIG. 3.—Cover object (as percentage of observations) for cottonmouths at Back Bay National Wildlife Refuge.

TABLE 10.--Sun exposure for cottonmouths at Back Bay National Wildlife Refuge. Sun exposure for mark-recapture snakes (NM-AF) and resight data for radiotelemetry snakes (AP-1-AP-5) were placed into three categories and compared using chi-square tests with Yates' continuity correction (Sokal and Rohlf, 1995). Appropriate alpha-levels and degrees of freedom (total chi-square: $\alpha = 0.05$, $df = 2$; partial chi-squares $\alpha = 0.01$, $df = 1$) are described in the text. Asterisks indicate statistical significance.

	NM	AM	NF	AF	AP-1	AP-2	AP-3	AP-4	AP-5
Full sun	32	15	18	8	15	42	28	8	5
Shade	7	2	0	3	2	9	31	9	9
Full shade	18	1	8	1	7	11	19	5	14
Total chi-square	15.20*	17.46*	16.70*	4.69	9.09*	31.10*	2.49	0.65	3.44
Full sun vs. Shade	14.77*	7.93*	16.06*	1.45	8.47*	20.08*	0.07	0.00	0.64
Full sun vs. Full shade	3.38	10.56*	3.12	4.00	2.23	16.98*	1.36	0.31	3.37
Shade vs. Full shade	4.00	0.00	6.125	0.25	1.78	0.05	2.42	0.64	0.70

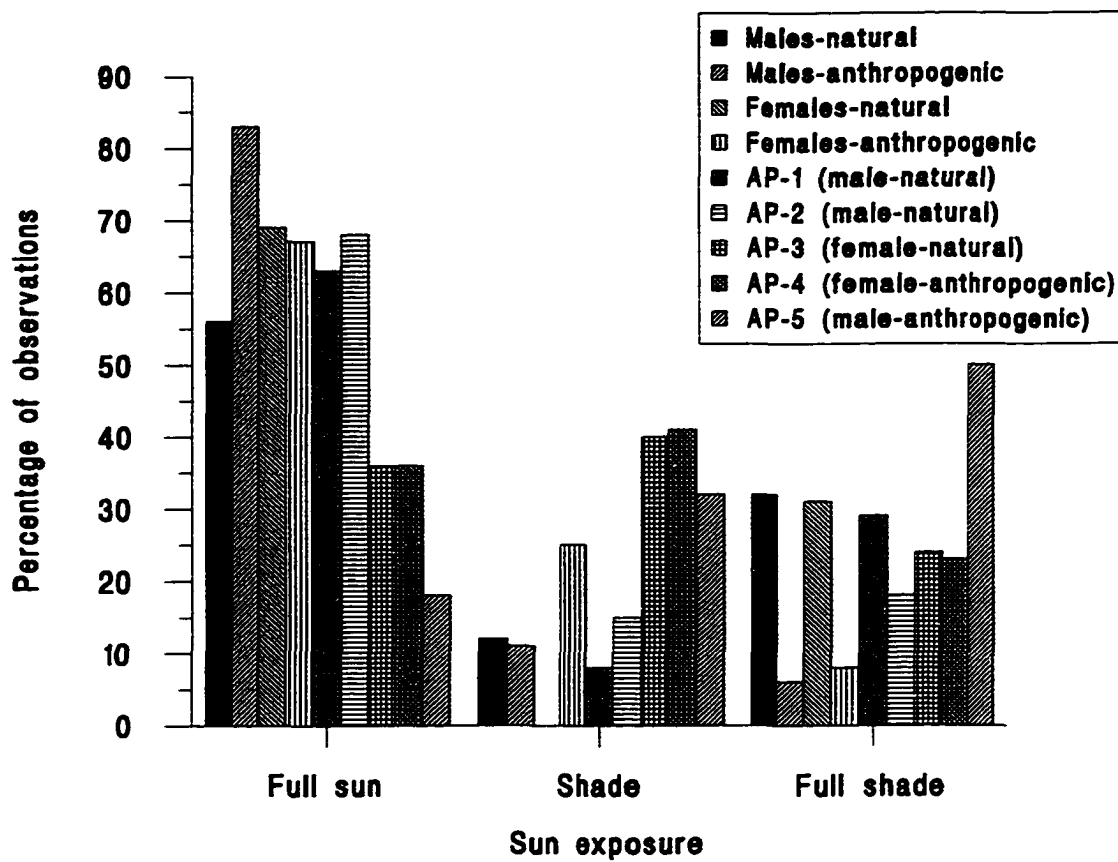


FIG. 4.--Sun exposure (as percentage of observations) for cottonmouths at Back Bay National Wildlife Refuge.

for males in the anthropogenic marsh (Table 12; Fig. 10). Most snakes remained in place when approached. No snakes below 18 C made any attempt to flee or approach. Flee and approach behaviors were most common for mark-recapture males, and approach only occurred with male snakes. All attempts to flee were made at temperatures > 21 C (Fig. 12-Fig. 10).

Defensive behavior.—Nearly all snakes were passive when approached, elevating and orienting the head toward the investigator rather than initiating aggressive behavior. A few snakes, however, were quite aggressive and struck readily, and most of these aggressive encounters were with large males (Table 13; Fig. 11). Aggressive behaviors occurred at all temperatures (Fig. 5-Fig. 8).

Population and reproductive data.—Sex ratios were skewed toward males in this study (see *Population Estimation*, below). Gravid females were not commonly captured. In 1996, 13.3 % (2 of 15) and 22.2% (2 of 9) of the females captured in the natural and anthropogenic marsh, respectively, were gravid. In 1997, 13.6% (3 of 22) and 9.5% (2 of 21) of the females captured in the natural and anthropogenic marsh, respectively, were gravid.

Uncaptured snakes.—A total of 53 located snakes evaded capture throughout the study. Most fled before the investigator was within capture distance. Snakes in the anthropogenic marsh fled much sooner than snakes in the natural marsh (natural marsh: $\bar{x} = 2.34$ m, $se = 0.157$, $n = 44$; anthropogenic marsh: $\bar{x} = 4.11$ m, $se = 0.820$, $n = 9$). However, a conservative t-test ($df = 8$, in accordance with the lowest n) did not reveal a significant difference in approach distance between natural and anthropogenic systems ($t = 2.12$, $P > 0.05$). The pooled mean approach distance was 2.64 m ($se = 0.206$).

A contingency table analysis was used to determine whether the approach medium (land or water) was independent of the medium to which the snake fled. The number of individuals in each category was similar (Table 14). The chi-square statistic ($\chi^2 = 0.027$, $df = 1$, $P > 0.05$) did not support the hypothesis that the approach medium affected the

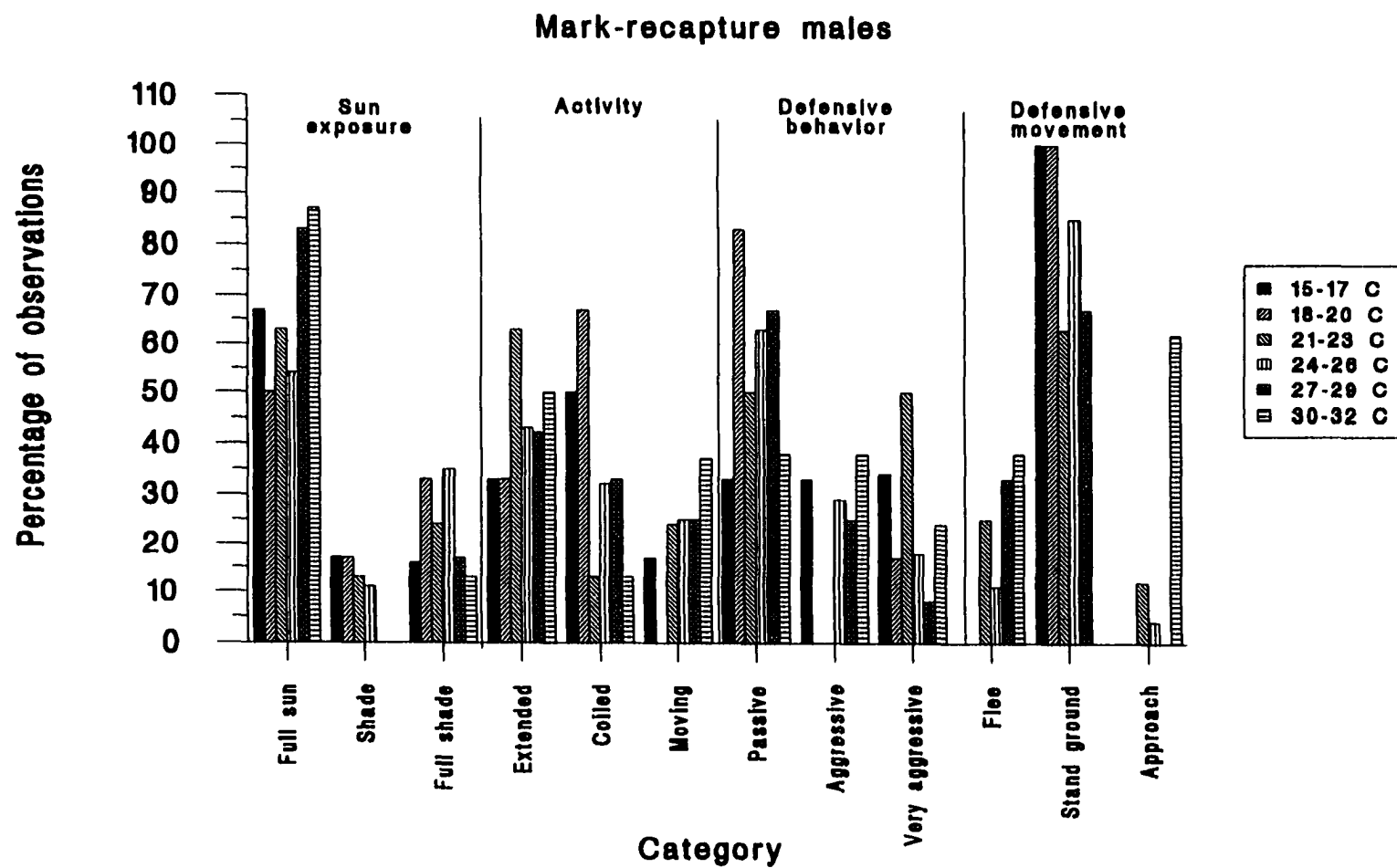


FIG. 5.--Percentage of observations for sun exposure, activity, defensive behavior, and defensive movement plotted by temperature for mark-recapture male cottonmouths at Back Bay National Wildlife Refuge.

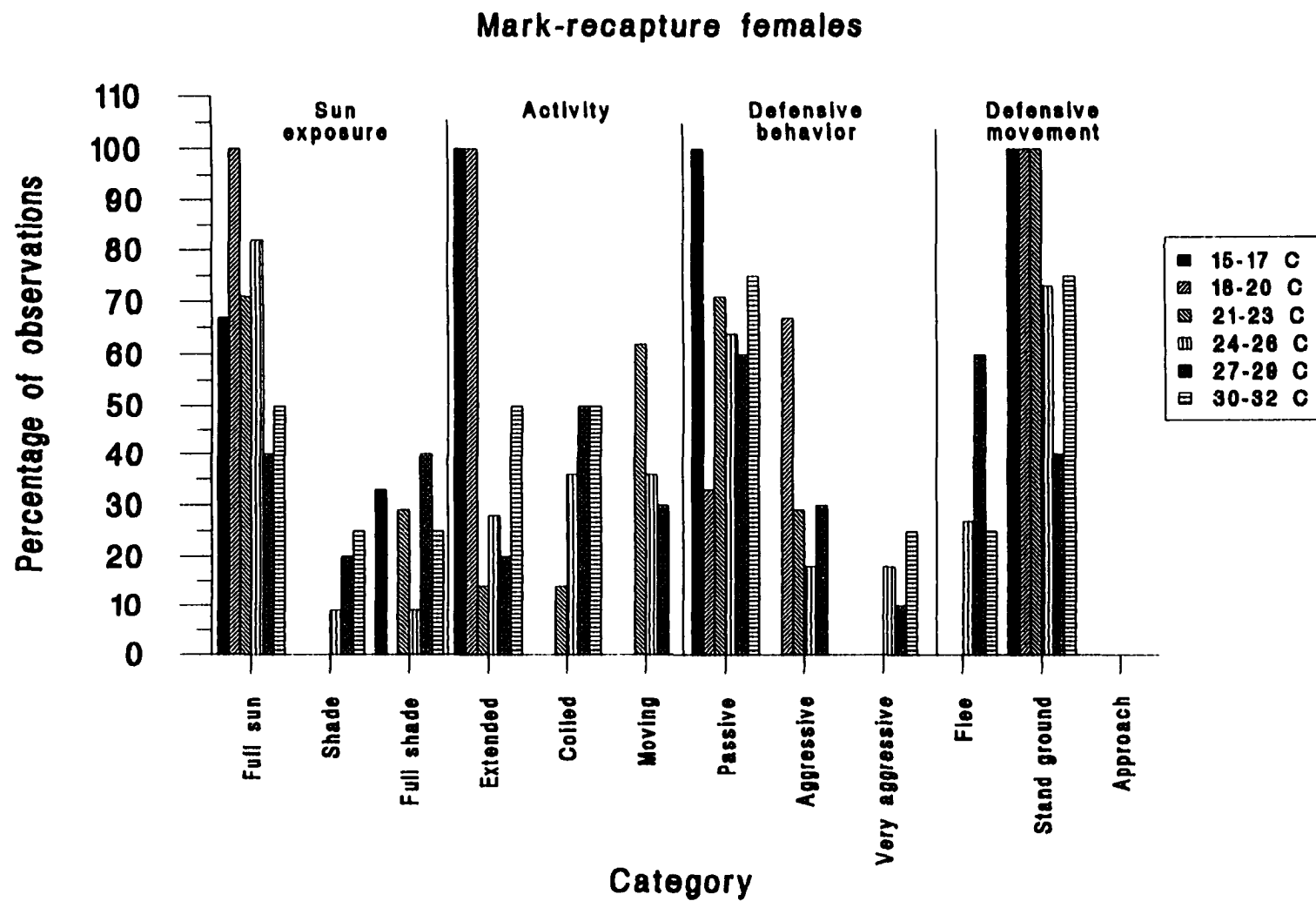


FIG. 6.--Percentage of observations for sun exposure, activity, defensive behavior, and defensive movement plotted by temperature for mark-recapture female cottonmouths at Back Bay National Wildlife Refuge.

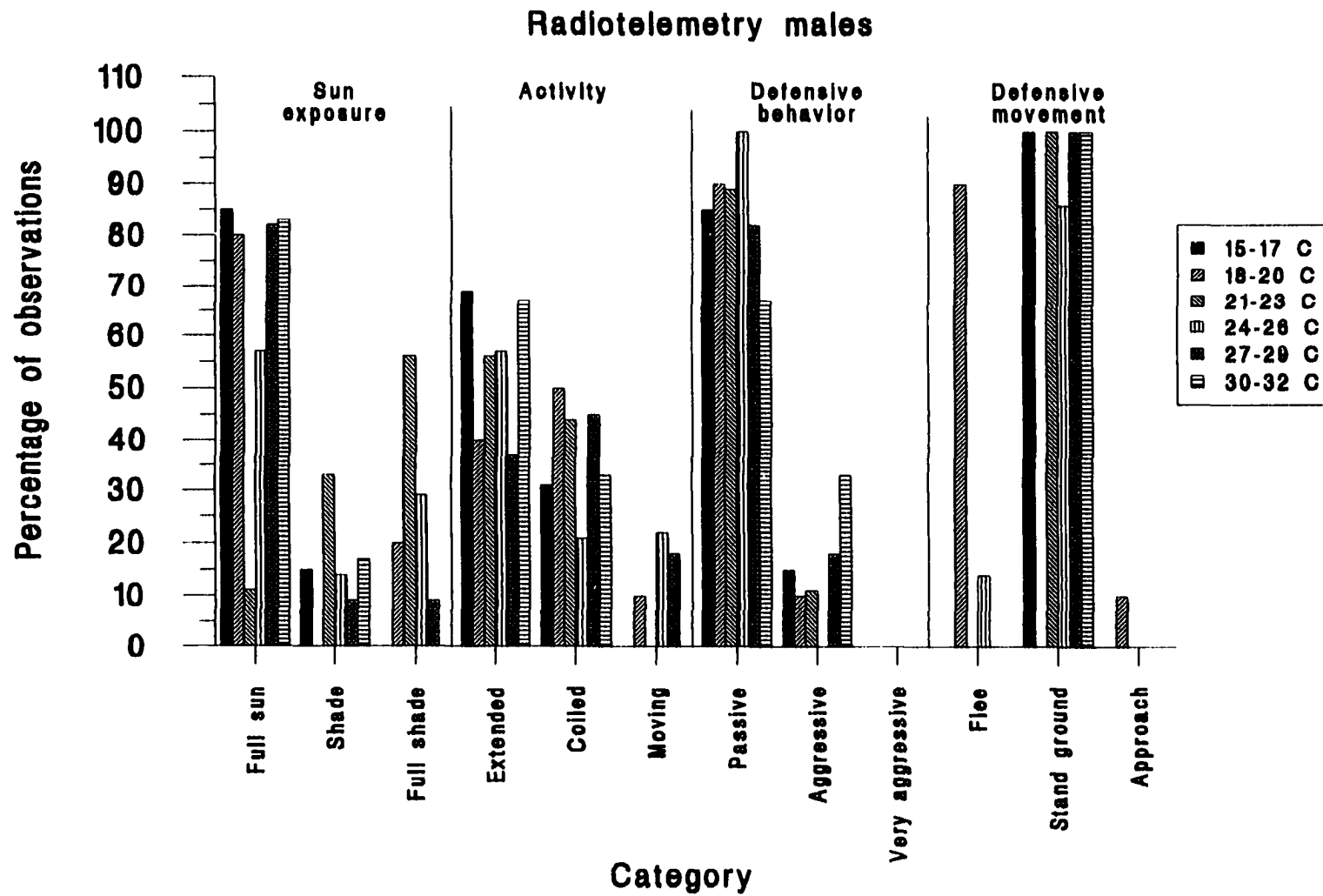


FIG. 7.--Percentage of observations for sun exposure, activity, defensive behavior, and defensive movement plotted by temperature for radiotelemetered male cottonmouths at Back Bay National Wildlife Refuge.

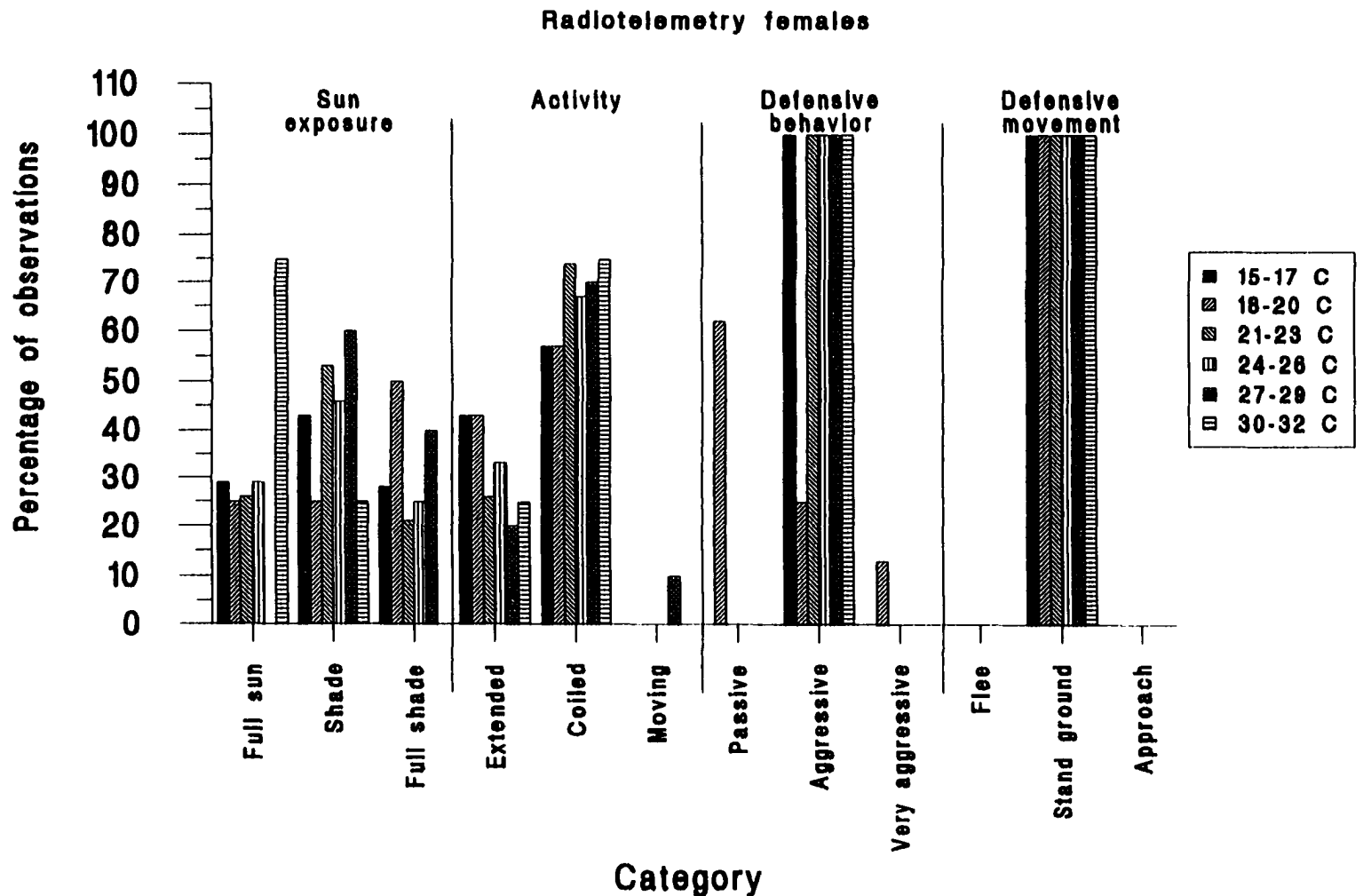


FIG. 8.--Percentage of observations for sun exposure, activity, defensive behavior, and defensive movement plotted by temperature for radiotelemetered female cottonmouths at Back Bay National Wildlife Refuge.

TABLE 11.--Activity for cottonmouths at Back Bay National Wildlife Refuge. Activity for mark-recapture snakes (NM-AF) and resight locations for radiotelemetry snakes (AP-1-AP-5) were placed into three categories and compared using chi-square tests with Yates' continuity correction (Sokal and Rohlf, 1995). Appropriate alpha-levels and degrees of freedom (total chi-square: $\alpha = 0.05$, $df = 2$; partial chi-squares $\alpha = 0.01$, $df = 1$) are described in the text. Asterisks indicate statistical significance.

	NM	AM	NF	AF	AP-1	AP-2	AP-3	AP-4	AP-5
Extended	23	8	9	5	15	43	24	5	5
Moving	13	6	5	3	2	1	2	2	5
Coiled	20	4	12	4	9	8	41	13	11
Total chi-square	2.25	0.79	2.09	0.19	8.32*	55.50*	32.45*	7.91*	2.39
Extended vs. Moving	2.25	0.07	0.64	0.13	8.47*	38.20*	16.96*	0.57	0.10
Extended vs. Coiled	0.09	0.75	0.19	0.00	1.04	22.67*	3.94	2.72	1.56
Moving vs. Coiled	5.65	0.10	2.30	0.00	3.27	4.00	33.58*	6.67*	1.56

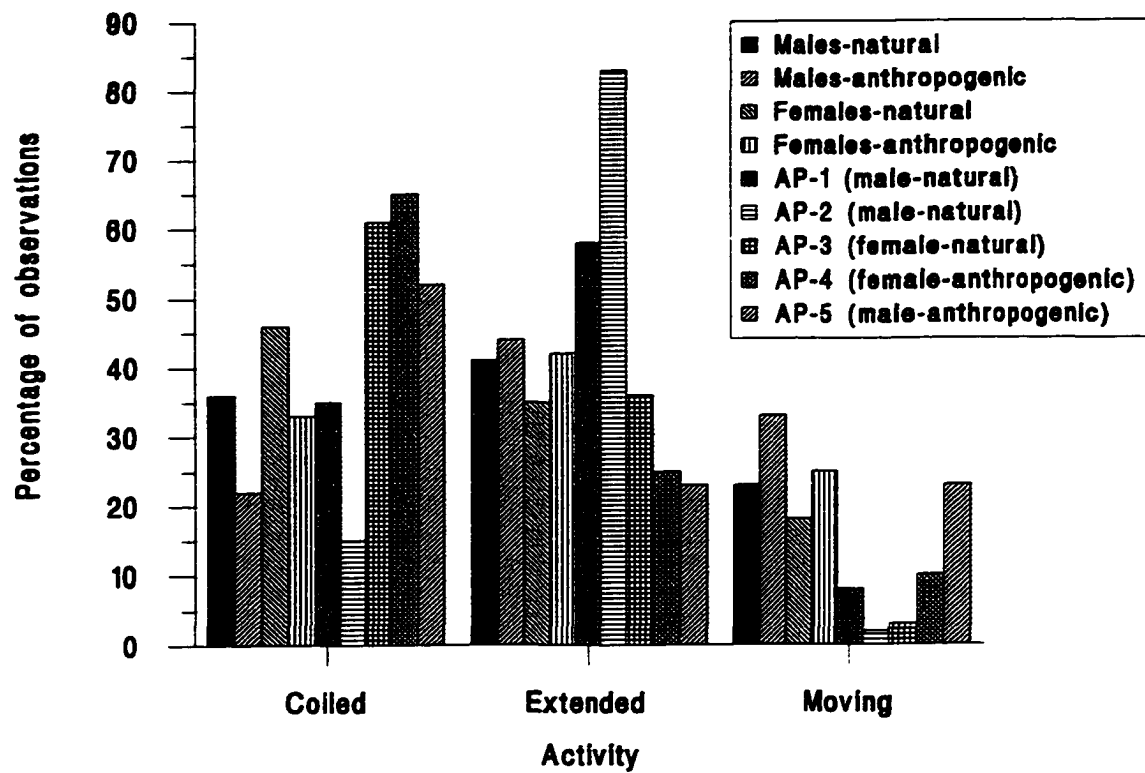


FIG. 9.--Activity (as percentage of observations) for cottonmouths at Back Bay National Wildlife Refuge.

TABLE 12.--Defensive movement for cottonmouths at Back Bay National Wildlife Refuge. Action data for mark-recapture snakes (NM-AF) and resight locations for radiotelemetry snakes (AP-1-AP-5) were placed into three categories and compared using chi-square tests with Yates' continuity correction (Sokal and Rohlf, 1995). Appropriate alpha-levels and degrees of freedom (total chi-square: $\alpha = 0.05$, $df = 2$; partial chi-squares $\alpha = 0.01$, $df = 1$) are described in the text. Asterisks indicate statistical significance.

	NM	AM	NF	AF	AP-1	AP-2	AP-3	AP-4	AP-5
Immobile	45	10	19	8	24	61	73	20	21
Flee	7	6	6	4	1	1	0	1	2
Approach	1	2	0	0	1	0	0	0	0
Total chi-square	61.39*	4.13	20.18*	6.19*	37.24*	114.23*	142.03*	32.68*	31.66*
Immobile vs. Flee	26.33*	0.56	5.76	0.75	19.36*	56.15*	71.01*	15.43*	14.09*
Immobile vs. Approach	40.20*	4.08	17.05*	6.13	19.36*	59.02*	71.01*	18.05*	19.05*
Flee vs. Approach	3.13	1.13	4.17	2.25	0.50	0.00	0.00	0.00	0.50

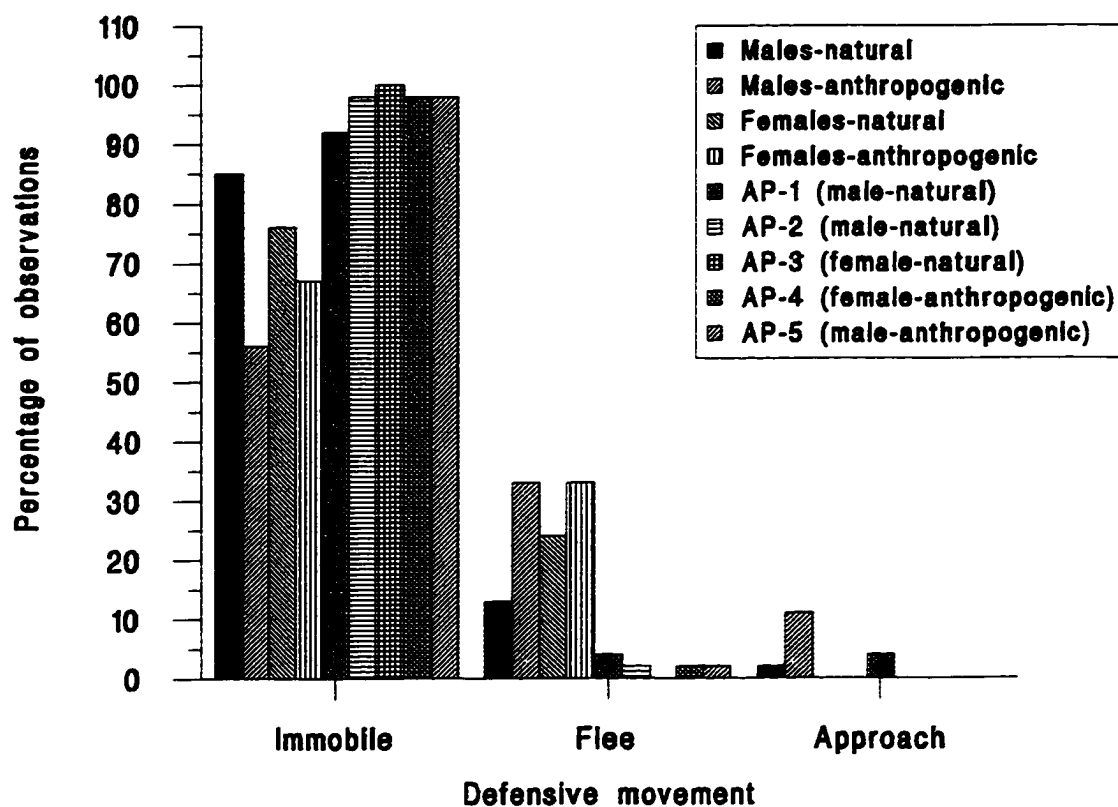


FIG. 10.--Defensive movement (as percentage of observations) for cottonmouths at Back Bay National Wildlife Refuge.

TABLE 13.--Defensive behavior data for cottonmouths at Back Bay National Wildlife Refuge. Behavior data for mark-recapture snakes (NM-AF) and resight data for radiotelemetry snakes (AP-1-AP-5) were placed into three categories and compared using chi-square tests with Yates' continuity correction (Sokal and Rohlf, 1995). Appropriate alpha-levels and degrees of freedom (total chi-square: $\alpha = 0.05$, $df = 2$; partial chi-squares $\alpha = 0.01$, $df = 1$) are described in the text. Asterisks indicate statistical significance.

	NM	AM	NF	AF	AP-1	AP-2	AP-3	AP-4	AP-5
Aggressive	12	6	6	3	3	10	5	1	1
Very aggressive	14	2	2	2	1	0	2	0	1
Passive	27	8	17	7	21	52	59	19	16
Total chi-square	6.49*	2.39	12.50*	2.19	28.01*	70.68*	90.22*	30.71*	25.61*
Aggressive vs. Very aggressive	0.04	1.13	1.13	0.00	0.25	8.1*	0.57	0.00	0.50
Aggressive vs. Passive	5.03	0.07	4.35	0.90	12.96*	27.11*	43.89*	14.45*	13.47*
Very aggressive vs. Passive	3.51	2.50	10.32*	1.78	17.39*	50.01*	51.41*	17.05*	13.47*

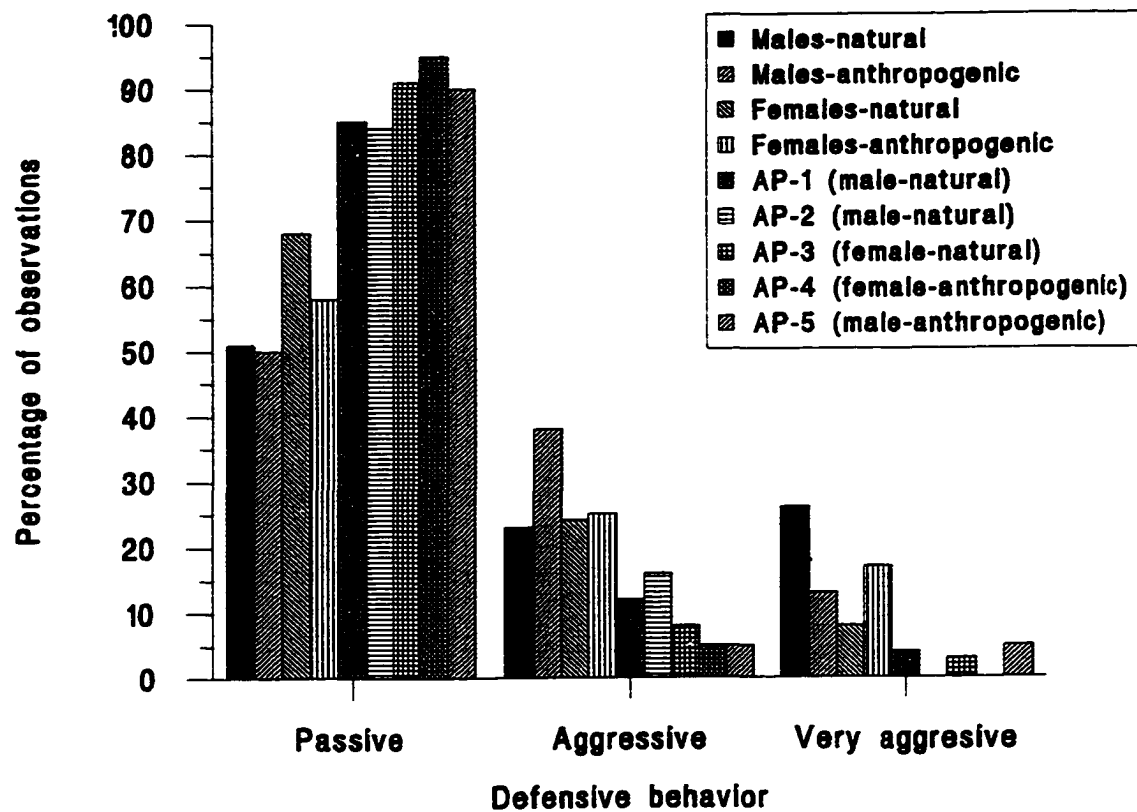


FIG. 11.—Defensive behavior (as percentage of observations) for cottonmouths at Back Bay National Wildlife Refuge.

TABLE 14.--Contingency table for 53 cottonmouths that escaped capture at Back Bay National Wildlife Refuge. Snakes from natural and anthropogenic marsh systems were pooled prior to analysis (see text). Data are presented according to the medium from which approach was made and to which medium the snake fled and subsequently evaded capture.

	Approach from land	Approach from water
Flee to land	14	13
Flee to water	14	12

escape medium. That is, the snake simply fled opposite the direction of approach no matter where it was or how it had been approached.

Habitat Analyses

Multiple comparisons.--Descriptive statistics for the eleven habitat variables revealed differences among each category examined (Table 15). In general, standard errors were small for all variables except vegetation density. Of particular interest was the seemingly low variation among both snake sites and random sites. For the results below, NM = natural marsh males, AM = anthropogenic marsh males, NF = natural marsh females, and AF = anthropogenic marsh females.

Distance to water (DW) did not differ between random sites in the natural and anthropogenic marsh systems, and mark-recapture animals did not differ between natural and anthropogenic marshes. However, both NM and NF were found closer to water than random north sites and AM and AF were found closer to water than random south sites, though no differences were found between natural marsh and anthropogenic marsh animals. Radio-tracked animals, on the other hand, showed surprising differences. Males and females radio-tracked in the natural marsh (NM and FM, respectively) showed no significant DW differences from random sites in the natural marsh, whereas the telemetered AM differed from random anthropogenic sites. The telemetered AF, however, did not differ from random anthropogenic marsh sites. Radiotracked snakes in the natural marsh were found significantly farther from water than mark-recapture snakes in the natural marsh, but those tracked in the anthropogenic marsh did not show differences when compared to mark-recapture animals in the anthropogenic marsh. The AM male (AP-5) was found significantly farther from water than were the radiotracked NM males (Table 16).

TABLE 15.—Means and standard errors (given in parentheses) of habitat variables for each snake or random category. Habitat variables are given in Table 2. Snake and random categories are given in Table 3.

	DW	DBO	DOT	DBU	DUT	CAN	LEAF	DEB	VEG	DENS	HT
RN	17.93 (3.46)	11.29 (0.43)	6.81 (1.43)	2.99 (0.16)	3.24 (0.76)	18.81 (2.76)	18.93 (3.08)	15.39 (1.97)	64.88 (3.71)	223.29 (19.85)	0.87 (0.06)
RA	19.41 (2.93)	14.53 (0.73)	13.36 (1.42)	2.23 (0.13)	12.19 (1.69)	12.66 (2.64)	11.16 (2.60)	16.90 (2.40)	56.44 (4.51)	169.29 (17.69)	0.55 (0.05)
NM	1.02 (0.48)	10.08 (0.52)	3.38 (0.85)	3.11 (0.24)	2.53 (0.65)	41.05 (6.68)	8.49 (3.18)	17.91 (4.70)	34.07 (6.74)	52.42 (12.90)	0.41 (0.09)
AM	1.01 (0.57)	11.92 (0.85)	15.06 (3.15)	6.27 (3.71)	8.91 (2.51)	0.00 (0.00)	0.59 (0.59)	13.23 (7.14)	23.53 (8.67)	52.65 (22.37)	0.34 (0.11)
NF	1.89 (0.76)	12.17 (1.44)	9.50 (4.50)	2.95 (0.37)	1.71 (0.24)	15.45 (6.68)	9.32 (5.26)	18.86 (7.26)	60.0 (9.26)	150.55 (39.23)	0.80 (0.16)
AF	0.52 (0.45)	10.73 (1.41)	13.64 (4.65)	2.69 (0.43)	7.73 (2.51)	7.27 (7.27)	7.27 (7.27)	1.82 (1.22)	24.09 (12.15)	125.91 (76.80)	0.67 (0.38)
AP-1	17.17 (2.53)	12.77 (0.62)	6.11 (1.82)	4.03 (0.26)	6.02 (1.83)	25.52 (7.29)	18.62 (5.44)	58.45 (8.19)	69.48 (8.54)	117.10 (16.23)	1.16 (0.17)
AP-2	13.27 (1.15)	9.65 (0.57)	4.68 (0.93)	3.80 (0.14)	1.29 (0.07)	4.46 (1.92)	34.11 (4.08)	34.38 (3.32)	84.02 (4.13)	159.73 (11.23)	1.11 (0.04)
AP-3	6.64 (0.85)	10.71 (0.43)	5.76 (1.02)	3.60 (0.25)	5.17 (1.04)	35.34 (5.55)	16.86 (4.05)	21.95 (3.38)	63.61 (5.85)	152.71 (16.13)	0.92 (0.12)
AP-4	2.44 (0.39)	12.93 (0.79)	8.35 (1.97)	2.63 (0.28)	3.94 (0.99)	26.14 (6.77)	18.18 (6.19)	20.0 (5.62)	72.73 (7.36)	279.55 (35.53)	1.50 (0.13)
AP-5	15.30 (10.30)	17.31 (1.45)	25.20 (13.54)	3.21 (0.20)	7.25 (3.30)	80.75 (7.92)	11.25 (6.14)	7.25 (3.93)	35.50 (10.64)	134.00 (43.79)	0.53 (0.15)

TABLE 16.--Results of Tukey's Studentized Range (HSD) Test for distance to water (m). Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.

	RN	RA	NM	AM	NF	AF	AP-1	AP-2	AP-3	AP-4	AP-5
RN	*										
RA	N	*									
NM	Y	Y	*								
AM	Y	Y	N	*							
NF	Y	Y	N	N	*						
AF	Y	Y	N	N	N	*					
AP-1	N	N	Y	Y	Y	Y	*				
AP-2	N	N	Y	Y	Y	Y	N	*			
AP-3	N	N	Y	Y	Y	Y	N	N	*		
AP-4	N	N	N	N	N	N	N	Y	N	*	
AP-5	Y	Y	N	N	N	N	Y	Y	Y	N	*

The diameter at breast height of the closest overstory tree (DBO) did not differ between random sites in the natural and anthropogenic marsh systems, nor did it differ between mark-recapture males and females in either marsh. Radiotracked snakes showed a similar pattern, except that AM AP-5 was nearer larger trees than NM AP-2. No differences were found between relevant comparisons of radio-tracked and mark-recapture animals (Table 17).

The distance to the nearest overstory tree (DOT) was significantly less for random sites in the natural and anthropogenic marshes. Additionally, NM and NF were found significantly closer to overstory trees than their anthropogenic marsh counterparts, but no differences were found among males or females when looking at individual marsh systems. Radiotracked snakes showed no differences in either system (Table 18).

The diameter at breast height of the nearest understory tree (DBU) did not differ between random sites in the natural and anthropogenic marshes. Radiotracked NM were nearer larger diameter understory trees than random sites in the natural marsh, but only male AP-2 differed from mark-recapture natural marsh males. The AM (AP-5) showed a similar condition when compared to random anthropogenic marsh sites, but the female did not. No significant differences were found among the mark-recapture classes (Table 19).

The distance to the nearest understory tree (DUT) was significantly greater in random anthropogenic marsh sites as compared to random natural marsh sites. Natural marsh males and females did not differ from random nor from each other, and the anthropogenic marsh snakes showed the same pattern. AM were significantly farther from understory trees than were NM and NF. Radio-tracked snakes showed no differences from random sites in their respective marsh systems (Table 20).

Percent canopy closure (CAN) was significantly higher in the natural marsh system than in the anthropogenic marsh. Neither NM and NF nor AM and AF differed from random sites in their respective marsh systems; however, mark-recapture NM were found

TABLE 17.—Results of Tukey's Studentized Range (HSD) Test for diameter at breast height of overstory tree (cm). Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.

	RN	RA	NM	AM	NF	AF	AP-1	AP-2	AP-3	AP-4	AP-5
RN	*										
RA	N	*									
NM	N	Y	*								
AM	N	N	N	*							
NF	N	N	N	N	*						
AF	N	N	N	N	N	*					
AP-1	N	N	Y	N	N	N	*				
AP-2	N	Y	N	N	N	N	Y	*			
AP-3	N	Y	N	N	N	N	N	N	*		
AP-4	N	N	N	N	N	N	N	N	N	*	
AP-5	Y	N	Y	N	N	N	N	Y	Y	N	*

TABLE 18.—Results of Tukey's Studentized Range (HSD) Test for distance to overstory tree (m). Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.

	RN	RA	NM	AM	NF	AF	AP-1	AP-2	AP-3	AP-4	AP-5
RN	*										
RA	Y	*									
NM	N	Y	*								
AM	Y	N	Y	*							
NF	N	Y	N	Y	*						
AF	N	N	Y	N	Y	*					
AP-1	N	Y	N	Y	N	N	*				
AP-2	N	Y	N	Y	N	N	N	*			
AP-3	N	Y	N	Y	N	N	N	N	*		
AP-4	N	N	Y	N	N	N	N	N	N	*	
AP-5	N	N	Y	N	N	N	N	N	N	N	*

TABLE 19.—Results of Tukey's Studentized Range (HSD) Test for diameter at breast height of understory tree (cm). Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.

	RN	RA	NM	AM	NF	AF	AP-1	AP-2	AP-3	AP-4	AP-5
RN	*										
RA	N	*									
NM	N	Y	*								
AM	N	N	N	*							
NF	N	N	N	N	*						
AF	N	N	N	N	N	*					
AP-1	Y	Y	N	Y	N	N	*				
AP-2	Y	Y	Y	Y	Y	N	N	*			
AP-3	N	Y	N	N	N	N	N	N	*		
AP-4	N	N	N	N	N	N	Y	Y	N	*	
AP-5	N	Y	N	N	N	N	N	N	N	N	*

TABLE 20.—Results of Tukey's Studentized Range (HSD) Test for distance to understory tree (m). Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.

	RN	RA	NM	AM	NF	AF	AP-1	AP-2	AP-3	AP-4	AP-5
RN	*										
RA	Y	*									
NM	N	Y	*								
AM	Y	N	Y	*							
NF	N	Y	N	Y	*						
AF	Y	N	Y	N	Y	*					
AP-1	N	N	N	N	N	N	*				
AP-2	N	Y	N	Y	N	Y	Y	*			
AP-3	N	N	N	Y	N	N	N	Y	*		
AP-4	N	N	N	N	N	N	Y	Y	N	*	
AP-5	N	N	N	N	N	N	N	N	N	N	*

in areas of much higher canopy cover than AM. The radiotelemetered NF was found with much less canopy cover than random sites in the natural marsh. The radiotelemetered AM was found in much higher canopy cover locations than random sites in the anthropogenic marsh system and male locations in the natural marsh. The radiotracked NF was found in areas of higher canopy closure than was NM AP-2 (Table 21).

Percent leaf litter cover (LEAF) was higher in the natural marsh compared to the anthropogenic marsh. Mark-recapture NM and AM were found in areas of less leaf cover than would be expected at random in their respective marshes. Radiotracked NM were found in areas of denser leaf cover than either random natural marsh sites or mark-recapture NM sites (Table 22).

Debris cover (DEB) did not differ between random sites in the two marshes, nor for mark-recapture animals; however, differences were seen in radiotelemetered snakes. Both AP-1 and AP-2 were found in areas of higher debris cover than the mark-recapture males in the natural marsh. The radiotracked AM was found in areas of significantly less debris cover than either AP-1 or AP-2 (Table 23).

No significant difference was found between random natural marsh and anthropogenic sites for vegetation cover (VEG). Mark-recapture NM and AM were found in areas of lower vegetation cover than their respective random sites. No differences were found between the sexes. Radiotracked NM were found in areas of higher vegetation cover than mark-recapture NM (Table 24).

Vegetation density (DENS) did not differ between random sites in natural and anthropogenic marshes. Mark-recapture NM and AM were found in areas of much lower vegetation density than their respective random sites. AP-2 used areas of higher vegetation density than the mark-recapture NM, and AP-4 used areas of higher vegetation cover than did AP-5 (Table 25).

Vegetation height (HT) was significantly greater in the natural marsh. Mark-recapture NM and AM were found in areas with lower vegetation height than random

TABLE 21.--Results of Tukey's Studentized Range (HSD) Test for percent canopy closure. Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.

	RN	RA	NM	AM	NF	AF	AP-1	AP-2	AP-3	AP-4	AP-5
RN	*										
RA	Y	*									
NM	N	Y	*								
AM	Y	N	Y	*							
NF	N	N	N	N	*						
AF	N	N	N	N	N	*					
AP-1	N	N	N	N	N	N	*				
AP-2	Y	N	Y	N	N	N	N	*			
AP-3	N	N	N	Y	N	N	N	Y	*		
AP-4	N	N	N	Y	N	N	N	Y	N	*	
AP-5	N	Y	Y	Y	Y	Y	Y	Y	Y	Y	*

TABLE 22.--Results of Tukey's Studentized Range (HSD) Test for percent leaf cover. Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.

	RN	RA	NM	AM	NF	AF	AP-1	AP-2	AP-3	AP-4	AP-5
RN	*										
RA	Y	*									
NM	Y	N	*								
AM	Y	N	N	*							
NF	N	N	N	N	*						
AF	N	N	N	N	N	*					
AP-1	Y	Y	Y	Y	Y	Y	*				
AP-2	Y	Y	Y	Y	N	Y	N	*			
AP-3	N	N	N	N	N	N	N	N	*		
AP-4	N	N	N	N	N	N	N	N	N	*	
AP-5	N	N	N	N	N	N	N	Y	N	N	*

TABLE 23.--Results of Tukey's Studentized Range (HSD) Test for percent debris cover. Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.

	RN	RA	NM	AM	NF	AF	AP-1	AP-2	AP-3	AP-4	AP-5
RN	*										
RA	N	*									
NM	N	N	*								
AM	N	N	N	*							
NF	N	N	N	N	*						
AF	N	N	N	N	N	*					
AP-1	Y	Y	Y	Y	Y	Y	*				
AP-2	Y	Y	Y	Y	Y	Y	N	*			
AP-3	N	N	N	N	N	N	N	N	*		
AP-4	N	N	N	N	N	N	Y	N	N	*	
AP-5	N	N	N	N	N	N	Y	Y	N	N	*

TABLE 24.--Results of Tukey's Studentized Range (HSD) Test for percent vegetation cover. Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.

	RN	RA	NM	AM	NF	AF	AP-1	AP-2	AP-3	AP-4	AP-5
RN	*										
RA	N	*									
NM	Y	N	*								
AM	Y	N	N	*							
NF	N	N	N	N	*						
AF	N	N	N	N	N	*					
AP-1	N	N	Y	Y	N	Y	*				
AP-2	Y	Y	Y	Y	N	Y	N	*			
AP-3	N	N	Y	Y	N	N	N	N	*		
AP-4	N	N	Y	Y	N	N	N	N	N	*	
AP-5	N	N	N	N	N	N	Y	Y	N	N	*

TABLE 25.—Results of Tukey's Studentized Range (HSD) Test for vegetation density (stems/m²) measurements. Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.

	RN	RA	NM	AM	NF	AF	AP-1	AP-2	AP-3	AP-4	AP-5
RN	*										
RA	N	*									
NM	Y	Y	*								
AM	Y	Y	N	*							
NF	N	N	N	N	*						
AF	Y	N	N	N	N	*					
AP-1	N	N	N	N	N	N	*				
AP-2	N	N	Y	Y	N	N	N	*			
AP-3	N	N	Y	Y	N	N	N	N	*		
AP-4	N	Y	Y	Y	Y	Y	Y	N	N	*	
AP-5	Y	N	N	N	N	N	N	N	N	Y	*

sites in their respective marshes. Radiotracked NM were found in areas of higher vegetation height than mark-recapture NM (Table 26).

Discriminant analysis.—The normal kernel density discriminant function analysis was well-suited to these data, as evidenced by the low number of classification errors (< 10%) for the discriminant functions developed by the analysis (Table 27). The canonical correlations generated by this analysis suggested that six of the 11 variables were most important in discrimination between categories (*viz.*, diameter at breast height of the nearest understory tree, distance to the nearest understory tree, distance to water, percent of leaf cover, percent vegetation cover, and percent canopy cover).

Polytomous logistic regression.—A plot of the number of grid cells against the percentage of total telemetry points allowed for use-intensity classes to be assigned. An obvious pattern can be seen in the graph, and this pattern suggested that three categories be used in the development of the model (Fig. 12). Of the 79 grid cells utilized by snakes, 39 were low-use grids (1-2%), 30 were medium-use grids (3-10%), and 10 were high-use grids (> 12%).

A forward selection procedure with $\alpha = 0.15$ selected four of the 11 variables as most important for delineating use-intensity classes. The four variables selected to be retained in the model were percent leaf cover (LEAF), distance to water (DW), distance to the nearest understory tree (DOT), and percent vegetation cover (VEG). The final model used was

$$L_i(\mathbf{X}) = \alpha_i + (0.029)DW + (0.046)DOT - (0.013)LEAF - (0.008)VEG.$$

Descriptive statistics for all 11 variables were computed for each use-intensity class for comparative purposes. Distance to water, percent leaf litter cover, and vegetation density had lowest means in the low-use category and highest means in the

TABLE 26.—Results of Tukey's Studentized Range (HSD) Test for stem height of dominant vegetation (m). Comparisons significant at $P = 0.05$ are indicated with a "Y" (Yes); insignificant comparisons are indicated with an "N" (No). Descriptions of abbreviations are given in Table 3.

	RN	RA	NM	AM	NF	AF	AP-1	AP-2	AP-3	AP-4	AP-5
RN	*										
RA	Y	*									
NM	Y	N	*								
AM	Y	N	N	*							
NF	N	N	N	N	*						
AF	N	N	N	N	N	*					
AP-1	N	Y	Y	Y	N	N	*				
AP-2	N	Y	Y	Y	N	Y	N	*			
AP-3	N	N	Y	N	N	N	N	Y	*		
AP-4	Y	Y	Y	Y	Y	Y	N	N	Y	*	
AP-5	N	N	N	N	N	N	N	Y	N	Y	*

TABLE 27.--Results of crossvalidation reclassification for the normal kernel density discriminant function analysis. Numbers shown are the percent of observations classified into a particular group (across the top of the table) from each category (down the left side). As an example, 99% of the RN observations were classified into the RN category, and 1% of the RN observations were classified into the AF category, given the discriminant function. Categories are described in Table 3.

	RN	RA	NM	AM	NF	AF	AP-1	AP-2	AP-3	AP-4	AP-5
RN	99	0	0	0	0	1	0	0	0	0	0
RA	0	100	0	0	0	0	0	0	0	0	0
NM	0	0	98	0	0	0	2	0	0	0	0
AM	0	0	0	94	0	6	0	0	0	0	0
NF	0	0	5	0	95	0	0	0	0	0	0
AF	0	0	0	0	0	100	0	0	0	0	0
AP-1	0	0	0	0	0	0	97	0	3	0	0
AP-2	0	0	0	0	0	0	0	100	0	0	0
AP-3	0	0	0	0	0	0	0	0	100	0	0
AP-4	0	0	0	0	0	0	0	0	0	100	0
AP-5	0	0	0	0	0	0	0	0	0	0	100

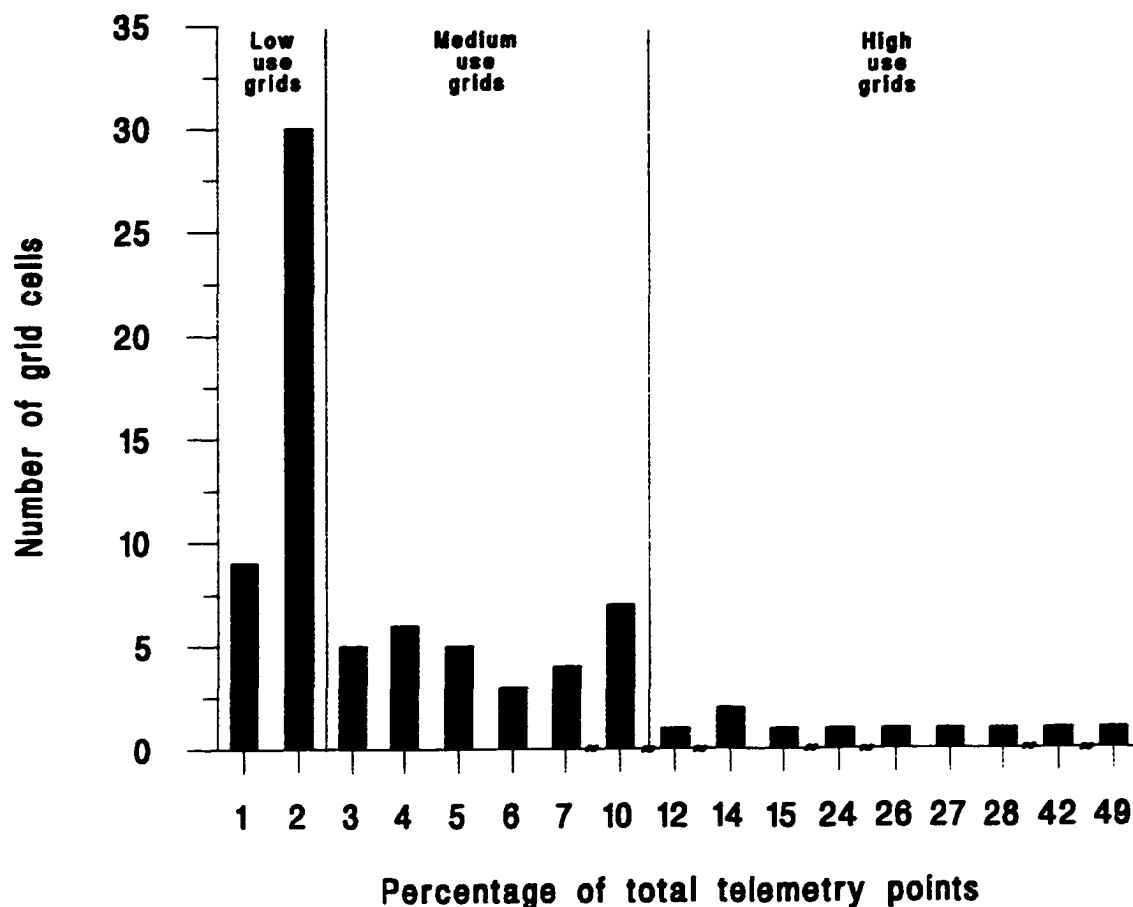


FIG. 12.—Pooled use-intensity categories for five radiotelemetered cottonmouths at Back Bay National Wildlife Refuge. Use is measured as the percentage of total telemetry locations of a snake that occur in a given grid cell.

high-use category; distance to the nearest understory tree showed the opposite trend (Table 28).

Classification errors, though slightly biased due to technique, were very good for the fitted model (Table 29). Over 70% of the observations were correctly classified into the proper use-intensity category.

Population Estimation

The zero-truncated Poisson test of equal catchability, testing the null hypothesis H_0 : equal catchability, could not be rejected in either year in either marsh. The critical χ^2 value with $\alpha = 0.05$ (d.f. = 1; 2 categories in each test) is $\chi^2_{(1), 0.05} = 3.84$. Calculated values for the natural marsh were $\chi^2 = 0.04$ and $\chi^2 = 0.25$ for 1996 and 1997, respectively, and in the anthropogenic marsh were $\chi^2 = 0.20$ and $\chi^2 = 0.02$ for 1996 and 1997, respectively. Therefore, snakes were considered to be equally catchable throughout this investigation.

Population estimates for 1996 were based on 109 captures of 100 animals, with 71 individual snakes and 7 recaptures occurring in the natural marsh and 29 individual snakes and 2 recaptures occurring in the anthropogenic marsh. Population estimates for 1997 were based on 135 captures of 122 animals, with 64 individual snakes and 11 recaptures occurring in the natural marsh and 58 individual snakes and 2 recaptures occurring in the anthropogenic marsh. Therefore, estimates for this study, with the restrictions detailed in the MATERIALS and METHODS, were based on 244 captures of 222 individuals.

Estimates of population size were always higher in the anthropogenic marsh (1996 = 366 snakes; 1997 = 477 snakes) than in the natural marsh (1996 = 314 snakes; 1997 = 154 snakes); however, confidence intervals were much wider for anthropogenic marsh estimates given the smaller number of recaptures in that system (Table 30). The difference in population size estimates was not statistically different at the $\alpha = 0.05$

TABLE 28.--Means and standard errors (in parentheses) for habitat variables for each use category in the polytomous logistic regression procedure. Habitat variables are given in Table 2. Category 1 = low-use grid cells, category 2 = medium-use grid cells, and category 3 = high-use grid cells. See text for description of technique and grid cell use selection criteria.

	DW (m)	DBO (cm)	DOT (m)	DBU (cm)	DUT (m)	CAN (%)	LEAF (%)	DEB (%)	VEG (%)	DENS (#/m ²)	HT (m)
1	5.24 (1.30)	12.99 (0.76)	14.18 (5.13)	3.24 (0.24)	7.69 (1.75)	21.92 (5.63)	13.08 (3.77)	22.95 (4.53)	65.64 (6.61)	203.21 (27.31)	1.12 (0.11)
2	6.81 (1.65)	11.98 (0.74)	7.46 (1.79)	3.40 (0.31)	4.86 (1.51)	28.47 (6.93)	24.04 (6.19)	26.04 (5.34)	67.14 (7.79)	172.76 (25.15)	0.94 (0.11)
3	16.45 (9.24)	14.01 (1.81)	3.50 (0.77)	2.85 (0.30)	2.20 (0.34)	29.00 (11.55)	35.00 (12.43)	29.50 (12.09)	75.00 (12.02)	166.50 (30.90)	1.26 (0.20)

TABLE 29.—Classification results for the polytomous logistic regression model. Numbers given are the percentage of observations classified into each category given the observed use-intensity level.

	Observed low-use category	Observed medium-use category	Observed high-use category
Predicted low-use category	80	20	0
Predicted medium-use category	33	67	0
Predicted high-use category	30	0	70

TABLE 30.—Population size and density estimates given as estimate [and 95% confidence interval] for cottonmouths at Back Bay National Wildlife Refuge. See text for explanation of calculation methods. Areal density based on a sampling area of 1200 ha in the natural marsh and 1900 ha in the anthropogenic marsh. Linear density based on a transect length of 6340 m in the natural marsh and 9860 m in the anthropogenic marsh.

	Natural Marsh		Anthropogenic Marsh	
	1996	1997	1996	1997
Population Estimate	314 [123, 679]	154 [75, 279]	366 [28, 1032]	477 [105, 1759]
Areal Density Estimate (number/ha)	0.26 [0.10, 0.57]	0.13 [0.06, 0.23]	0.19 [0.01, 0.54]	0.25 [0.06, 0.93]
Linear Density Estimate (number/m)	0.05 [0.02, 0.11]	0.02 [0.01, 0.04]	0.04 [0.002, 0.10]	0.05 [0.01, 0.18]

significance level in either year (1996: $z = 0.203$, $P > 0.80$; 1997: $z = 1.56$, $P > 0.10$).

Population density estimates were similar for both marsh systems, with linear density estimates being almost identical (Table 30).

Observed sex ratios were skewed toward males in both marshes for both years. In 1996 the sex ratio (M:F) was 56:15 ($\chi^2 = 22.54$, $P < 0.05$) in the natural marsh and 20:9 ($\chi^2 = 3.45$, $P > 0.05$) in the anthropogenic marsh. In 1997 the ratio (M:F) was 47:22 ($\chi^2 = 5.64$, $P < 0.05$) in the natural marsh and 37:21 ($\chi^2 = 3.88$, $P < 0.05$) in the anthropogenic marsh.

Foraging and Feeding Ecology

A total of 56 stomachs were examined for contents during this study. The number of females was equal for both areas, but more males were represented in the natural marsh than in the anthropogenic marsh (Table 31). A majority of the stomachs examined contained food items or liquid material. A weighted average (weighted by the numbers of snakes in each category) of only 35% of examined stomachs were empty (Table 31 and Table 32).

Twenty stomachs contained liquid with a slurry of nearly fully digested prey. Green frogs (*Rana clamitans*) were the most common food item, followed closely by sunfish (*Lepomis* spp.) and southern leopard frogs (*R. utricularia*). Only one stomach contained mammalian remains (*Microtus* sp.). Reptilian prey was found in three stomachs, one containing a northern water snake (*Nerodia sipedon*) and two containing turtles (evidenced from the shape of the food bolus; they were not palped out of stomachs due to the possibility of injuring the snakes). Twenty stomachs had nonfood items, including rocks, sand, dirt, vegetation, and wood material (Table 31). A large male snake was seen in a slow and presumably predatory approach of a plover (*Charadrius* spp.), but the bird escaped before a strike was made. A large female cottonmouth was seen swallowing a

TABLE 31.—Summary of food items collected from cottonmouths at Back Bay National Wildlife Refuge. Data are presented as total number of items per category, separated by marsh area and sex.

Food item category	Natural marsh males (n = 23)	Natural marsh females (n = 9)	Anthropogenic marsh males (n = 15)	Anthropogenic marsh females (n = 9)
Pisces				
<i>Lepomis</i> spp.	2	1	1	0
Amphibia				
<i>Rana clamitans</i>	2	1	1	2
<i>Rana utricularia</i>	2	0	0	1
Reptilia				
<i>Nerodia sipedon</i>	1	0	0	0
turtle (unidentifiable)	2	0	0	0
Mammalia				
<i>Microtus</i> spp.	0	0	1	0
Insecta				
unidentifiable	0	0	1	0
Miscellaneous				
rock	0	0	1	1
sand/dirt	3	3	4	2
wood material	1	0	1	0
plant material	3	1	2	0
Liquid	4	4	7	5
Empty (no gut contents)	8	4	5	1

TABLE 32.—Mean mass, volume, or dimensions (and standard errors) of items collected from cottonmouths at Back Bay National Wildlife Refuge. Food item data are in grams, liquid item data are in milliliters, and empty stomachs are given as a percentage of the total. Turtle mass was not determined; however, carapace dimensions were estimated in the field in millimeters.

Food item category	Natural marsh males (n = 23)	Natural marsh females (n = 9)	Anthropogenic marsh males (n = 15)	Anthropogenic marsh females (n = 9)
Pisces				
<i>Lepomis</i> spp.	12.0 g (0.01)	28.0 g (0)	35.1 g (0)	0
Amphibia				
<i>Rana clamitans</i>	26.5 g (23.24)	22.5 g (0)	10 g (0)	18.2 g (3.20)
<i>Rana utricularia</i>	31.0 g (12.55)	0	0	20.0 g (0)
Reptilia				
<i>Nerodia sipedon</i>	28.02 g (0)	0	0	0
turtle (unidentifiable)	40 mm X 40 mm 54 mm X 40 mm	0	0	0
Mammalia				
<i>Microtus</i> spp.	0	0	8.46 g (0)	0
Insecta				
unidentifiable	0	0	1	0
Miscellaneous				
rock	0	0	5.0 g (0)	7.2 g (0)
Liquid	11.3 ml (1.25)	16.8 ml (2.84)	11.3 ml (2.67)	12.0 ml (3.00)
Empty (no gut contents)	35%	44%	33%	11%

large *Rana clamitans*. The frog, which was being swallowed by the posterior end first, was still alive and delivered a loud distress call.

Given the broad range of prey species reported for cottonmouths (Allen and Swindell, 1948; Wharton, 1969; Gloyd and Conant, 1990; Ernst, 1992; Mitchell, 1994), potential prey items at BBNWR include many species of birds, mammals, fishes, amphibians and reptiles. Many surveys of fauna at BBNWR were carried out by the principal investigator and the biologists at BBNWR. Bird surveys of the refuge suggested that there were many possible avian prey species, but no bird remains were found in snake stomachs. Amphibian surveys suggested a density of 2.1 frogs/ m², with a majority (> 90%) of the captures being green frogs. Fish surveys revealed many possible prey species, but only absolute numbers were given by the BBNWR surveyors, so densities are not reported.

Radiotelemetry

Movements.—Five adult snakes were tracked for varying amounts of time from Autumn 1996 to Spring 1998 (Fig. 13-Fig. 17). The female tracked in the natural marsh (AP-3) was tracked for the longest time (208 days) before dying during autumn 1997. The female underwent two surgeries due to radio failures and may have succumbed to the resulting stress. The other female (AP-4) was in the anthropogenic marsh and died during hibernation. The two males in the natural marsh (AP-1 and AP-2) appeared healthy throughout the duration of their tracking, but were lost presumably due to radio failure. The male in the anthropogenic marsh (AP-5) survived and ultimately underwent surgical removal of the transmitter.

The number of days the animals were tracked varied from 83-208, with 54-101 observations made per snake. Though cottonmouths are often reported to be very active during the spring and summer (Wharton, 1969; Gloyd and Conant, 1990; Mitchell, 1994),

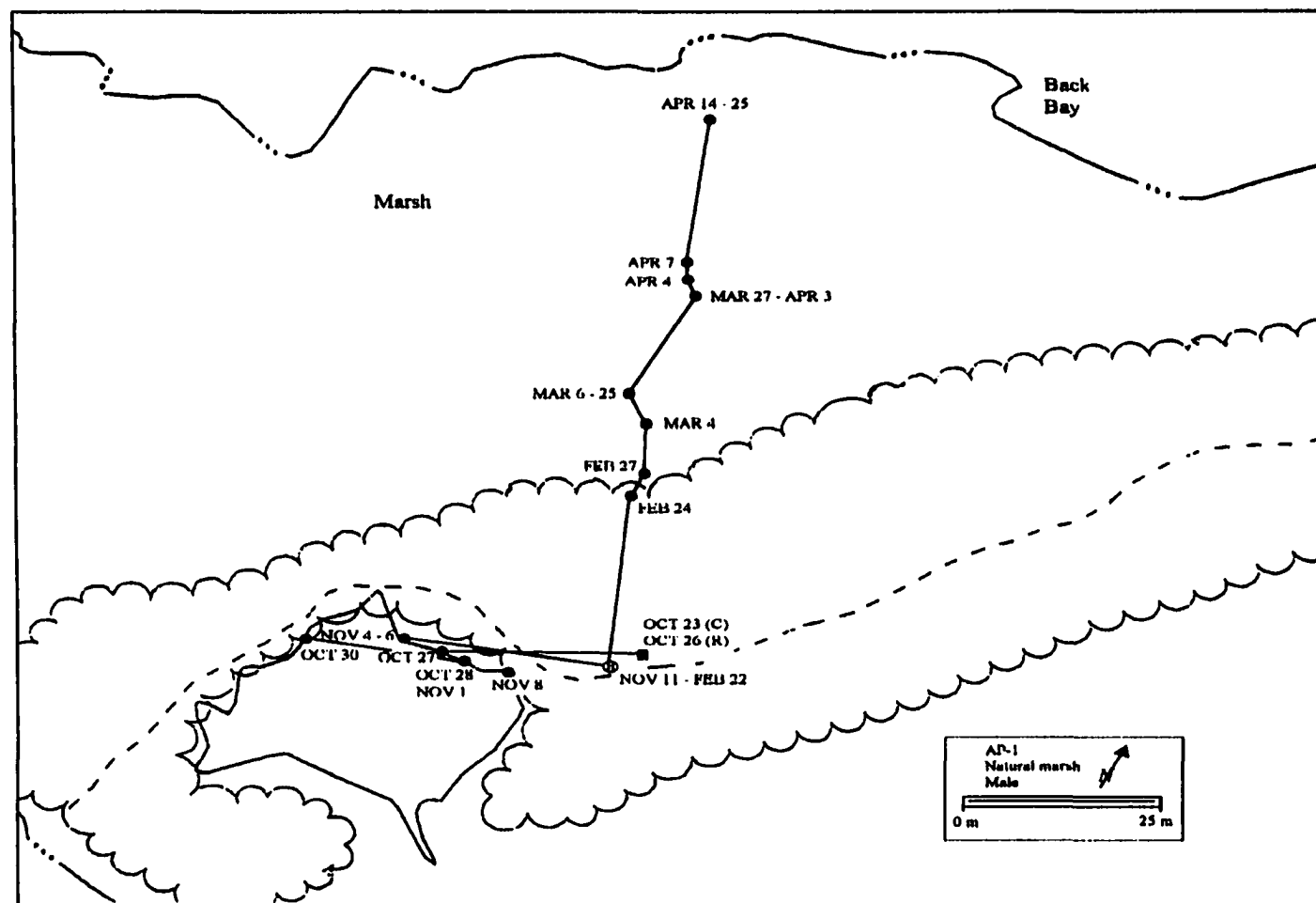


FIG. 13.--Movement map for subject AP-1 (male) in the natural marsh at Back Bay National Wildlife Refuge. The capture and release site is shown as a square, movement locations are shown as dots, and the hibernaculum is shown as a circled "H." Dates are shown for locations. Unlabeled areas on map shown by curved lines indicate low-lying marsh shrubs.

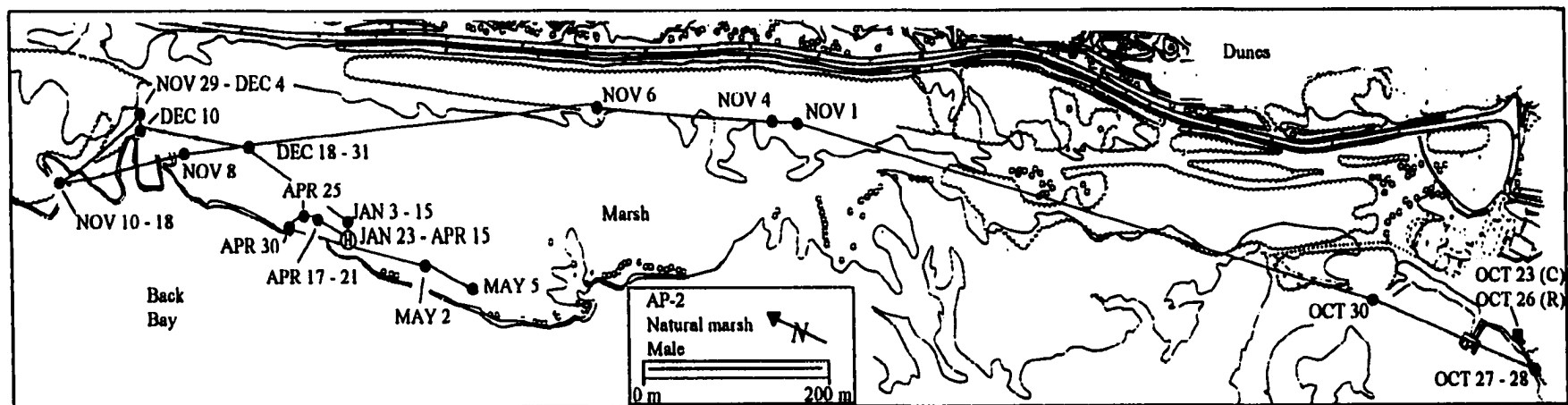


FIG. 14.--Movement map for subject AP-2 (male) in the natural marsh at Back Bay National Wildlife Refuge. The capture and release site is shown as a square, movement locations are shown as dots, and the hibernaculum is shown as a circled "H." Dates are shown for locations. Unlabeled areas on map shown by curved lines indicate low-lying marsh shrubs.

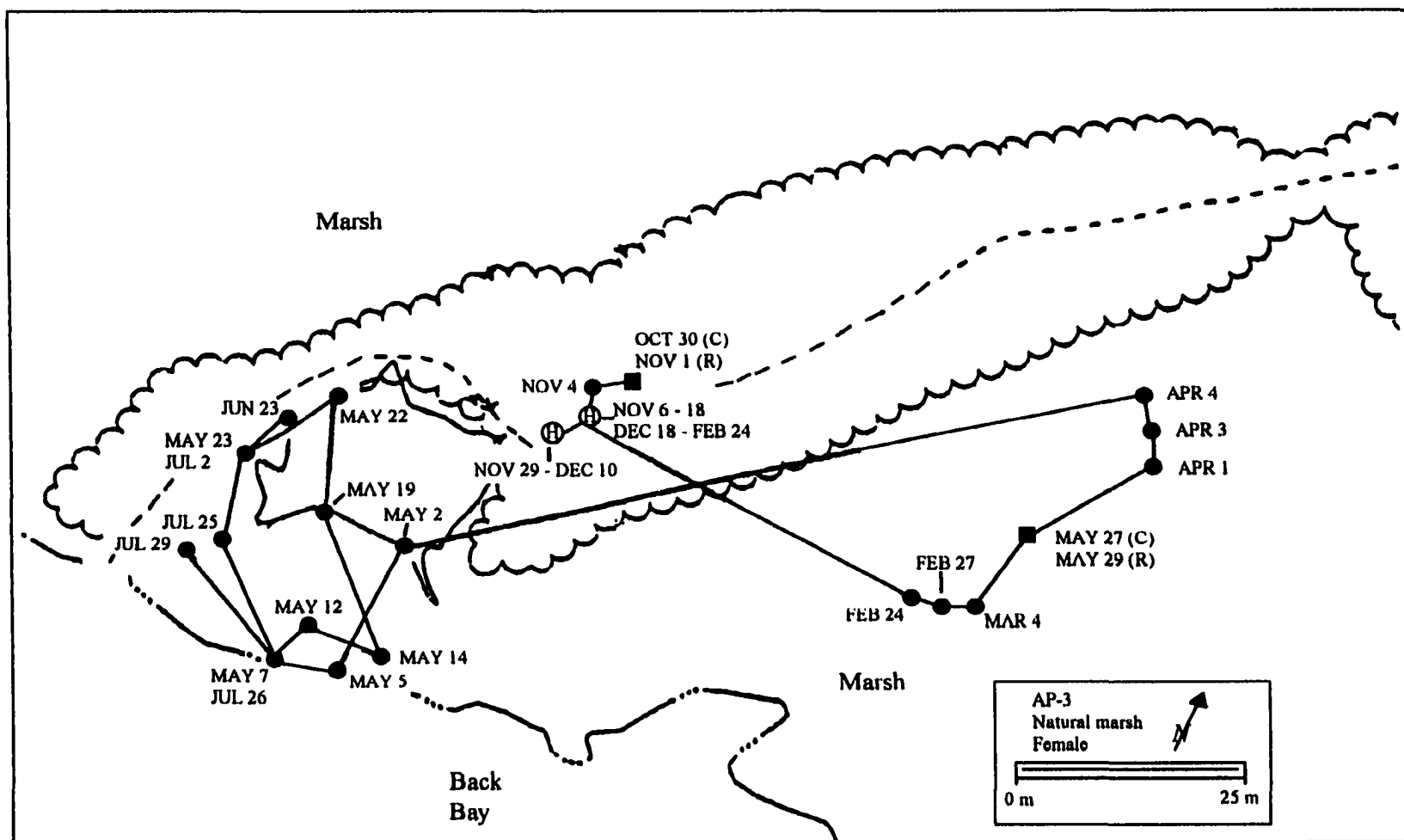


FIG. 15.--Movement map for subject AP-3 (female) in the natural marsh at Back Bay National Wildlife Refuge. The capture and release site is shown as a square, movement locations are shown as dots, and the hibernaculum is shown as a circled "H." Dates are shown for locations. Unlabeled areas on map shown by curved lines indicate low-lying marsh shrubs.

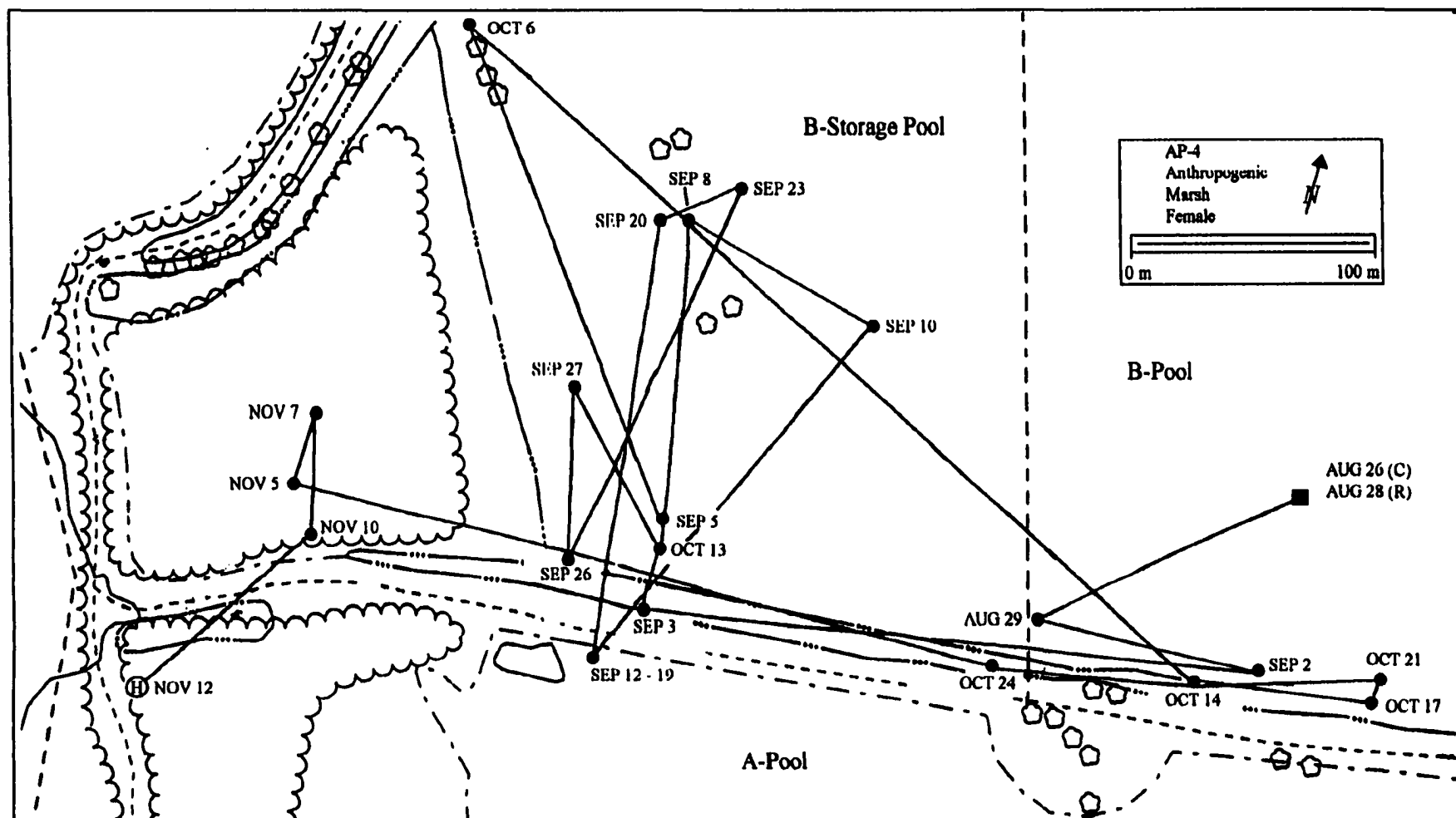


FIG. 16.--Movement map for subject AP-4 (female) in the anthropogenic marsh at Back Bay National Wildlife Refuge. The capture and release site is shown as a square, movement locations are shown as dots, and the hibernaculum is shown as a circled "H." Dates are shown for locations. Unlabeled areas on map shown by curved lines indicate forested sites.

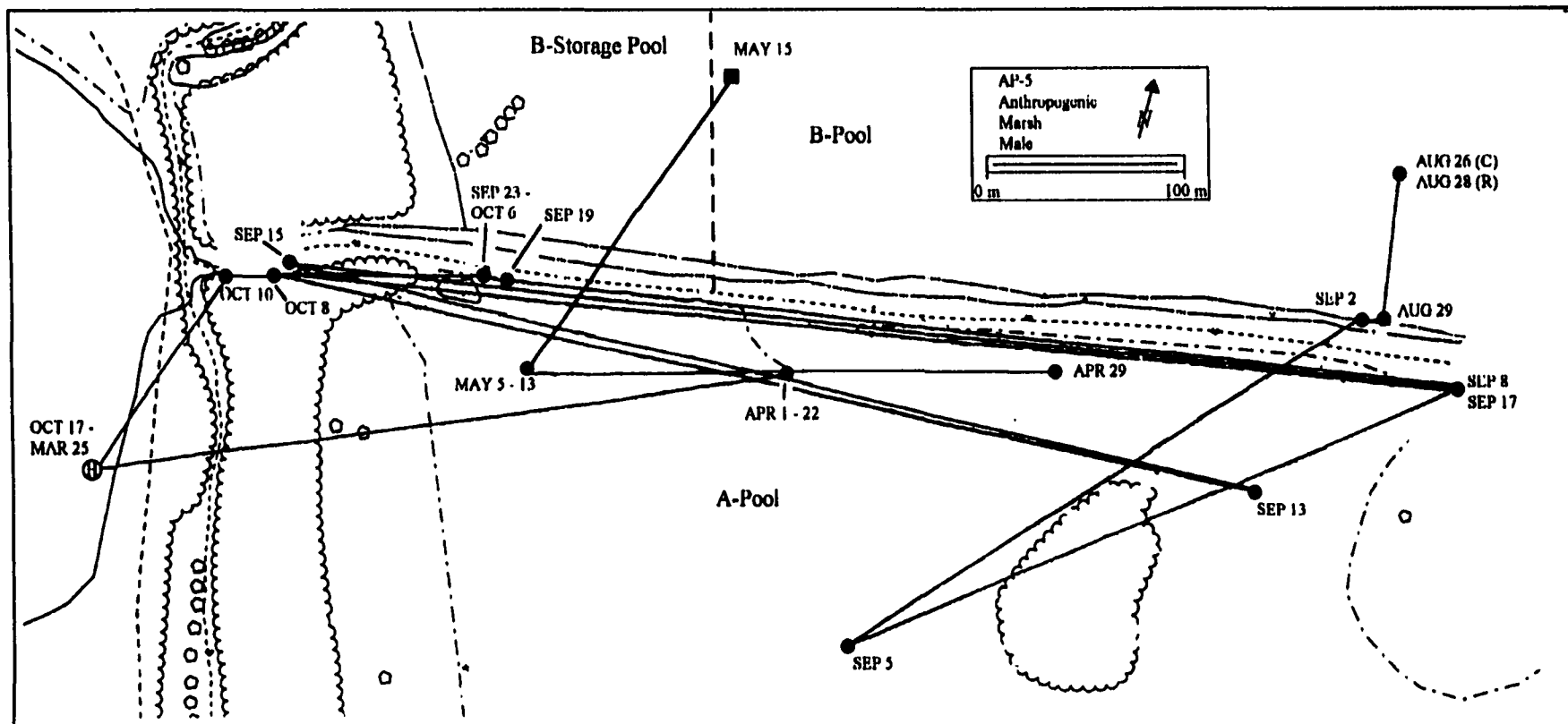


FIG. 17.--Movement map for subject AP-5 (male) in the anthropogenic marsh at Back Bay National Wildlife Refuge. The capture and release site is shown as a square, movement locations are shown as dots, and the hibernaculum is shown as a circled "H." Dates are shown for locations. Unlabeled areas on map shown by curved lines indicate forested sites.

few movements were observed for either sex in either marsh. Total distance moved was low for one male in the natural marsh (AP-1), but was much higher for the other male in that habitat (AP-2). The longest total distance moved was by the male in the anthropogenic marsh (AP-5). The longest daily movement was by AP-2, which moved approximately 640 m in a 24 hour period. Mean distance per day and mean distance per movement varied widely, but were highest for the males tracked in both systems (Table 33).

Activity areas and range lengths were variable. The smallest activity area and range length was for male AP-1 in the natural marsh (Table 34; Fig. 13), whereas the largest activity area and range length was for the other male in that system (AP-2; Table 34; Fig. 14). The female in the natural system had a much larger range length and greater activity range (AP-4; Table 34; Fig. 16) than did the female in the natural marsh (AP-3; Table 34; Fig. 15). The male in the anthropogenic marsh did not have a large activity range area or range length (AP-5; Table 34; Fig. 17), though it did have the highest total distance moved. As Fig. 17 shows, that snake made most of its movements in a linear fashion within a narrow impoundment ditch. Estimated activity range areas for recaptured snakes fell within the sizes recorded for radiotelemetered snakes. Males had overall greater mean than females, though female sample size was low (Table 35).

Subject AP-2 (Fig. 14) did not enter an underground hibernaculum but made several very long movements to a location where it spent several weeks under dense vegetation. Snakes AP-1, AP-3, and AP-5 (Fig. 18-Fig. 22) exhibited similar patterns of movements. Large movements were made immediately following egress from hibernacula and were followed by a long period of low activity. The areas where the snakes moved were similar in that they were characterized by very dense vegetation and high amounts of direct sunlight. Shedding took place in these areas before the snakes moved to new locations. Both females (AP-3, Fig. 15 and AP-4, Fig. 16) made movements to second

TABLE 33.--Movements of radiotracked snakes at Back Bay National Wildlife Refuge during the active season. Marsh location and sex are indicated by the following abbreviations: NM = male in natural marsh, AM = male in anthropogenic marsh, NF = female in natural marsh, and AF = female in anthropogenic marsh.

Subject	Number of days tracked	Number of observations	Number of movements	Total distance moved (m)	Mean distance moved per day (m/day)	Mean distance per movement (m)
AP-1 (NM)	83	54	15	230.40	2.78	15.36
AP-2 (NM)	102	67	16	2388.04	230.41	149.25
AP-3 (NF)	208	101	21	677.80	3.26	32.28
AP-4 (AF)	119	74	21	1517.78	12.75	72.28
AP-5 (AM)	149	73	15	4359.09	29.26	290.61

TABLE 34.—Activity range areas and range lengths for radiotracked snakes at Back Bay National Wildlife Refuge. Marsh location and sex are indicated by the following abbreviations: NM = male in natural marsh, AM = male in anthropogenic marsh, NF = female in natural marsh, and AF = female in anthropogenic marsh.

Subject	Harmonic mean 95% isopleth (ha)	Minimum convex polygon (ha)	Range length (m)
AP-1 (NM)	0.108	0.48	124.80
AP-2 (NM)	1545.00	638.75	1675.26
AP-3 (NF)	3.620	5.56	216.67
AP-4 (AF)	67.94	54.54	290.00
AP-5 (AM)	3.79	3.25	668.18

TABLE 35.--Minimum convex polygon activity areas of recaptured snakes at Back Bay National Wildlife Refuge. Male and female overall means (SE) are given.

Snake sex and marsh	Snout-vent length (mm)	Activity area (ha)
Female (natural)	561	0.054
Female (natural)	710	4.081
Female (natural; gravid)	604	0.066
Female (anthropogenic)	602	2.751
Male (natural)	807	2.093
Male (natural)	807	1.590
Male (natural)	970	0.031
Male (natural)	476	2.344
Male (natural)	672	2.894
Male (natural)	831	5.599
Male (natural)	742	4.797
Male (natural)	1002	6.511
Male (natural)	818	0.065
Male (natural)	752	1.130
Male (natural)	844	1.465
Male (natural)	782	7.976
Male (anthropogenic)	819	2.188
Female mean (all)		1.738 (1.116)
Male mean (all)		2.976 (0.603)

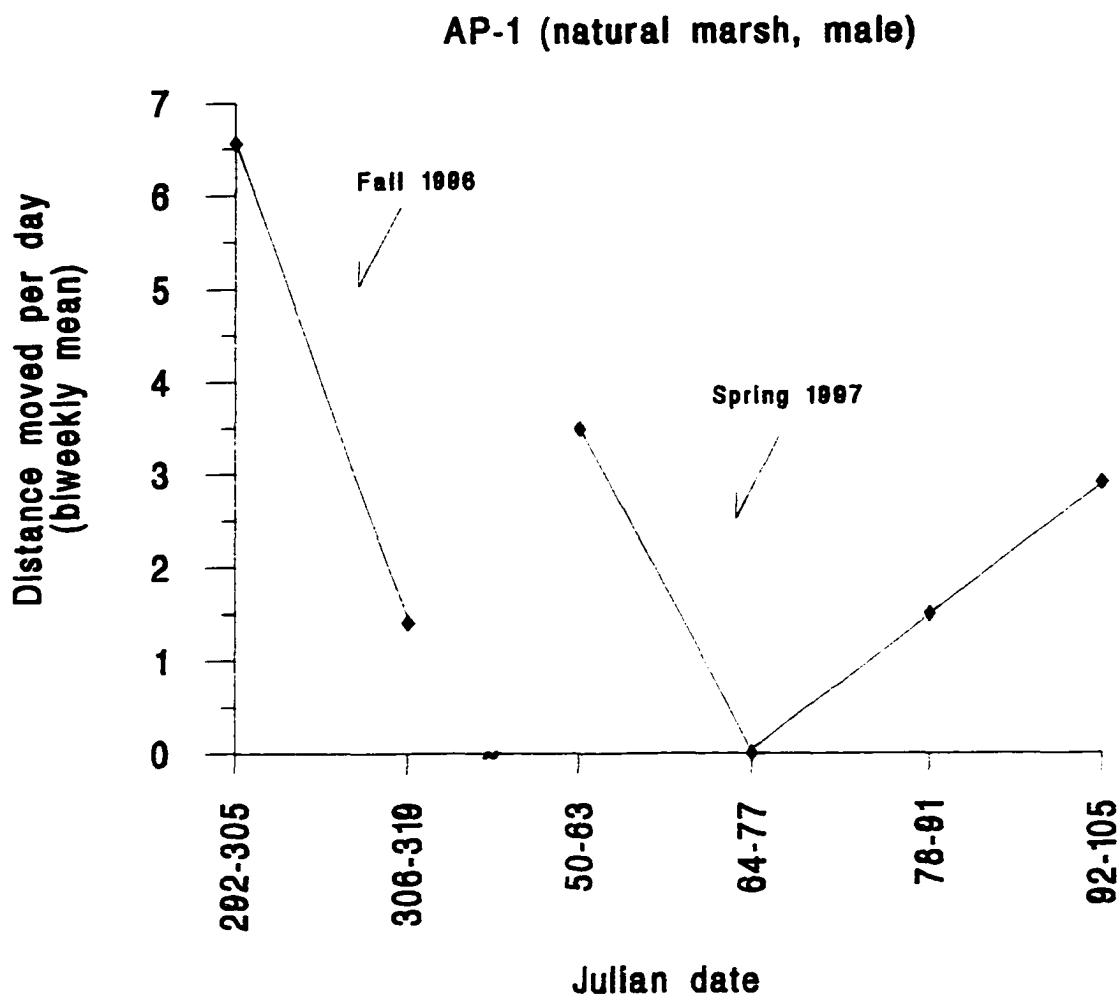


FIG. 18.—Distance moved per day (biweekly mean) for subject AP-1 (natural marsh, male) at Back Bay National Wildlife Refuge. The chart shows biweekly movements against Julian date both prior to ingress into the hibernaculum, and after egress from the hibernaculum. Season and year are given.

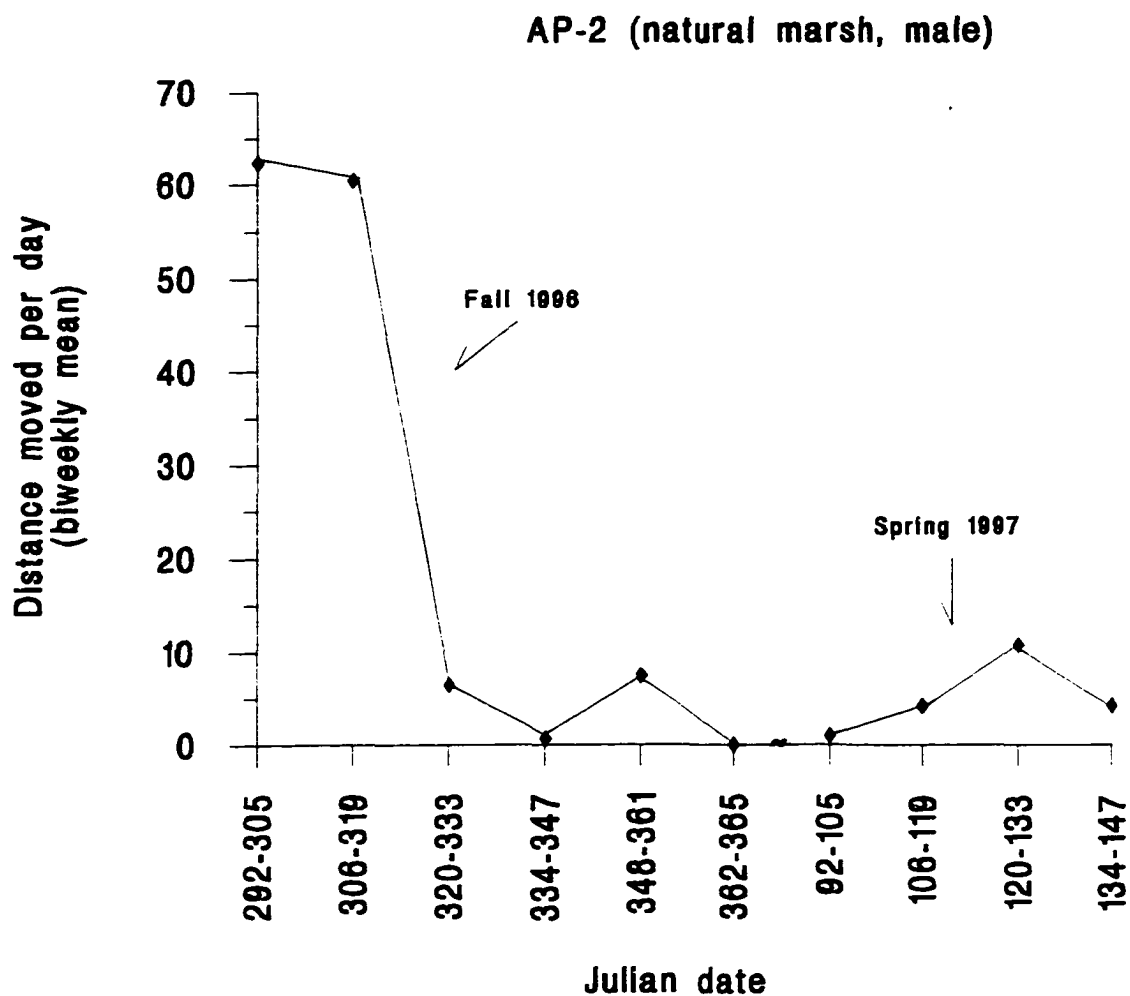


FIG. 19.--Distance moved per day (biweekly mean) for subject AP-2 (natural marsh, male) at Back Bay National Wildlife Refuge. The chart shows biweekly movements against Julian date both prior to ingress into the hibernaculum, and after egress from the hibernaculum. Season and year are given.

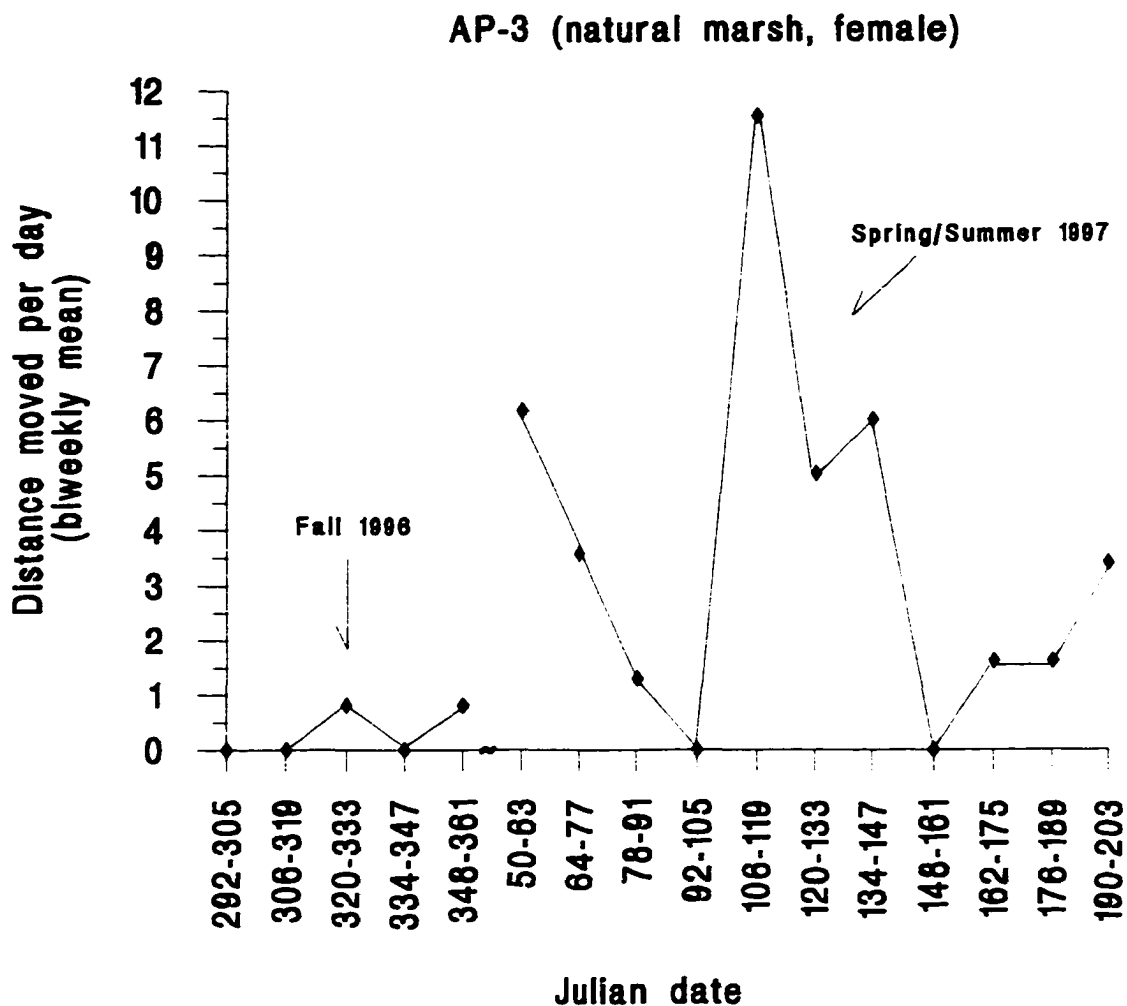


FIG. 20.—Distance moved per day (biweekly mean) for subject AP-3 (natural marsh, female) at Back Bay National Wildlife Refuge. The chart shows biweekly movements against Julian date both prior to ingress into the hibernaculum, and after egress from the hibernaculum. Season and year are given.

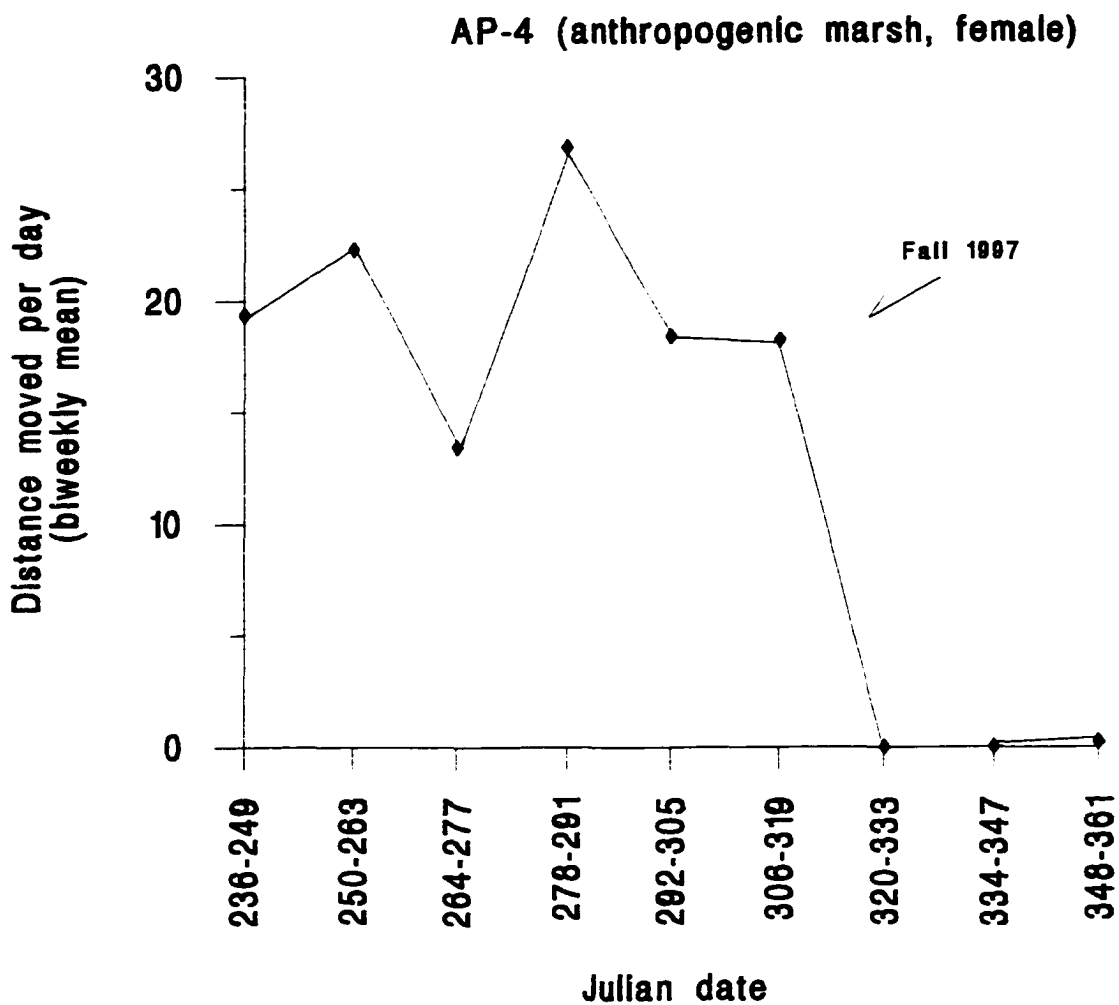


FIG. 21.--Distance moved per day (biweekly mean) for subject AP-4 (anthropogenic marsh, female) at Back Bay National Wildlife Refuge. The chart shows biweekly movements against Julian date both prior to ingress into the hibernaculum, and after egress from the hibernaculum. Season and year are given.

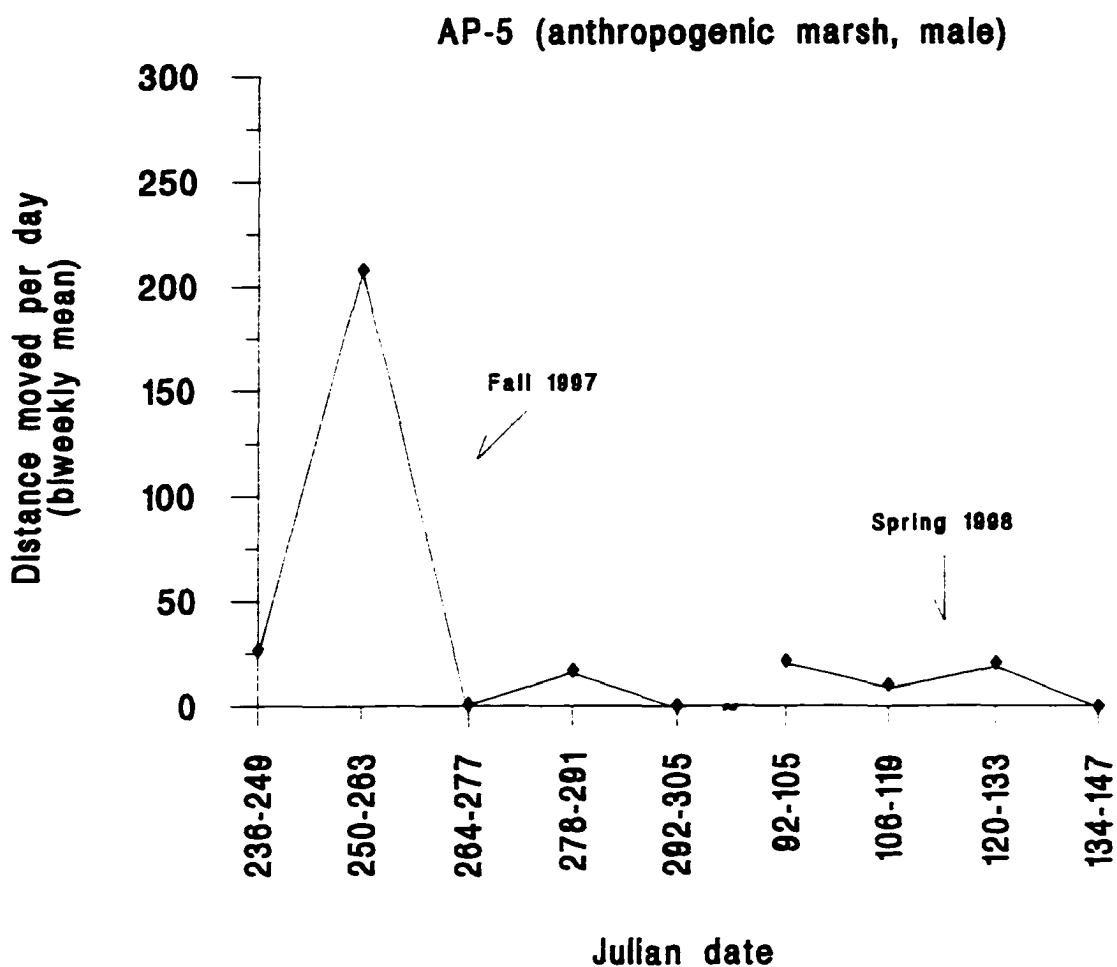


FIG. 22.—Distance moved per day (biweekly mean) for subject AP-5 (anthropogenic marsh, male) at Back Bay National Wildlife Refuge. The chart shows biweekly movements against Julian date both prior to ingress into the hibernaculum, and after egress from the hibernaculum. Season and year are given.

hibernacula during the winter, but AP-3 returned to the original hibernaculum 11 days after the initial move.

Temperature.—Mean body temperature for each snake during the active season was slightly less than air and surface temperatures, but higher than soil temperature (Table 36). During hibernation, overall mean body temperature remained higher than all three environmental temperatures, except for subject AP-2, which did not enter an underground hibernaculum and had a body temperature much lower than either air or surface temperature (Table 37). The highest recorded body temperature during the active season was for subject AP-5 (31.10 C), and the lowest body temperature during hibernation was for subject AP-1 (2.32 C).

Body temperature was highly correlated with all three environmental temperatures during the active season, with the highest weighted mean correlation (0.87) being between body and surface temperatures. During hibernation, the highest weighted mean correlation was with soil temperature. Not surprisingly the snake that did not seek underground shelter, AP-2, was the exception, with body temperature most highly correlated with air and surface temperatures (Table 38).

All five snakes entered hibernation when both air and surface temperatures fell below soil temperature, following an approximately four week overall decline in mean environmental temperatures. In most cases the snakes' body temperatures were higher than all three environmental temperatures at ingress. Interestingly, subject AP-2 went under heavy vegetation under similar temperature profile conditions. The four weeks prior to egress were characterized by an overall increase in all three environmental temperatures. At the time of egress, both air and surface temperatures were higher than soil temperature (Fig. 23-Fig. 27).

Female AP-3 moved twice during the hibernation period. The first move was 19 days after ingress. For the season her body temperature was relatively high (16.25 C), as were the air, surface, and soil temperatures (17.9 C, 16.3 C. and 14.8 C, respectively).

TABLE 36.—Mean body and environmental temperatures (C) for five radiotracked snakes at Back Bay National Wildlife Refuge during the active season. Marsh location and sex are indicated by the following abbreviations: NM = male in natural marsh, AM = male in anthropogenic marsh, NF = female in natural marsh, and AF = female in anthropogenic marsh. Data are presented as \bar{x} (n , SE).

Subject	Body temperature	Air temperature	Surface temperature	Soil temperature
AP-1 (NM)	14.21 (20, 5.247)	19.47 (20, 7.393)	15.45 (20, 5.187)	10.64 (20, 2.849)
AP-2 (NM)	15.10 (28, 8.541)	18.32 (28, 10.403)	15.79 (28, 8.680)	12.09 (28, 4.566)
AP-3 (NF)	20.95 (67, 5.985)	25.25 (67, 7.321)	21.94 (67, 5.990)	18.44 (67, 5.081)
AP-4 (AF)	19.92 (27, 5.488)	20.91 (27, 7.273)	19.28 (27, 6.645)	18.67 (27, 4.910)
AP-5 (AM)	21.20 (34, 4.876)	20.48 (34, 6.926)	19.29 (34, 5.532)	18.57 (34, 4.174)
Weighted mean	19.14 (176, 6.017)	21.90 (176, 7.736)	19.30 (176, 6.339)	16.60 (176, 4.544)

TABLE 37.—Mean body and environmental temperatures (C) for five radiotracked snakes at Back Bay National Wildlife Refuge during hibernation. Marsh location and sex are indicated by the following abbreviations: NM = male in natural marsh, AM = male in anthropogenic marsh, NF = female in natural marsh, and AF = female in anthropogenic marsh. Data are presented as \bar{x} (n , SE).

Subject	Body temperature	Air temperature	Surface temperature	Soil temperature
AP-1 (NM)	10.75 (25, 2.993)	9.35 (25, 5.054)	9.54 (25, 5.010)	9.26 (25, 2.414)
AP-2 (NM)	13.14 (24, 6.908)	18.15 (24, 7.355)	15.50 (24, 5.669)	9.62 (24, 2.696)
AP-3 (NF)	9.59 (25, 1.373)	9.42 (25, 4.962)	9.60 (25, 4.920)	9.20 (25, 2.402)
AP-4 (AF)	11.16 (39, 2.824)	9.52 (39, 5.244)	8.90 (39, 4.318)	10.23 (39, 2.677)
AP-5 (AM)	12.08 (32, 2.080)	7.67 (32, 4.211)	8.08 (32, 3.441)	11.13 (32, 1.722)
Weighted mean	11.35 (145, 3.115)	10.49 (145, 5.284)	10.04 (145, 4.571)	9.98 (145, 2.377)

TABLE 38.--Correlations for body temperature versus environmental temperatures during both the active season and hibernation for five radiotracked snakes at Back Bay National Wildlife Refuge. Marsh location and sex are indicated by the following abbreviations: NM = male in natural marsh, AM = male in anthropogenic marsh, NF = female in natural marsh, and AF = female in anthropogenic marsh. Data are presented as \bar{x} (n , SE)

Subject	Active season			Hibernation		
	Air temperature	Surface temperature	Soil temperature	Air temperature	Surface temperature	Soil temperature
AP-1 (NM)	0.67 (20, 0.175)	0.85 (20, 0.124)	0.55 (20, 0.197)	0.47 (25, 0.184)	0.45 (25, 0.186)	0.78 (25, 0.130)
AP-2 (NM)	0.89 (28, 0.089)	0.93 (28, 0.072)	0.93 (28, 0.072)	0.86 (24, 0.109)	0.83 (24, 0.119)	0.77 (24, 0.136)
AP-3 (NF)	0.78 (67, 0.078)	0.86 (67, 0.063)	0.84 (67, 0.067)	0.31 (25, 0.198)	0.27 (25, 0.201)	0.58 (25, 0.170)
AP-4 (AF)	0.84 (27, 0.109)	0.82 (27, 0.114)	0.89 (27, 0.091)	0.77 (39, 0.105)	0.78 (39, 0.103)	0.79 (39, 0.101)
AP-5 (AM)	0.86 (34, 0.090)	0.91 (34, 0.073)	0.92 (34, 0.069)	0.58 (32, 0.149)	0.63 (32, 0.142)	0.80 (32, 0.110)
Weighted mean	0.81 (176, 0.044)	0.87 (176, 0.037)	0.84 (176, 0.041)	0.61 (145, 0.066)	0.61 (145, 0.066)	0.75 (145, 0.055)

Her second move, back to the original hibernaculum, took place during an extremely cold period 11 days later (air temperature = 6.22 C, surface temperature = 5.7 C, and soil temperature = 8.0 C), and at a relatively low body temperature (8.11 C). Female AP-4 moved once after initial ingress. Her body temperature was 11.43 C, and air, surface, and soil temperatures (13.0 C, 10.7 C, and 9.3 C) were relatively high.

Visitor and Hunter Reports

Many more snakes were reported by visitors to BBNWR in 1996 than in 1997. The number of sightings peaked in June and July of 1996, and in May of 1997. Cottonmouths were commonly reported, but so were snakes referred to as "moccasins," thereby making it difficult to discern if the visitor was reporting a cottonmouth or a water snake (*Nerodia* sp.). Snakes in the "other" category included black racers (*Coluber constrictor*), hognose snakes (*Heterodon platyrhinos*), rough green snakes (*Opheodrys aestivus*), and black rat snakes (*Elaphe obsoleta*). One copperhead was reported by a visitor, though this snake does not occur at BBNWR (Fig. 28).

The 1997 survey of the hunters at BBNWR resulted in many reports of snakes. Most of these reports were of cottonmouths, but also included the snakes listed in the "other" category (see above). Again the term "moccasin" was used by several hunters and was plotted separately from the cottonmouth. One hunter reported seeing a juvenile copperhead (Fig. 29).

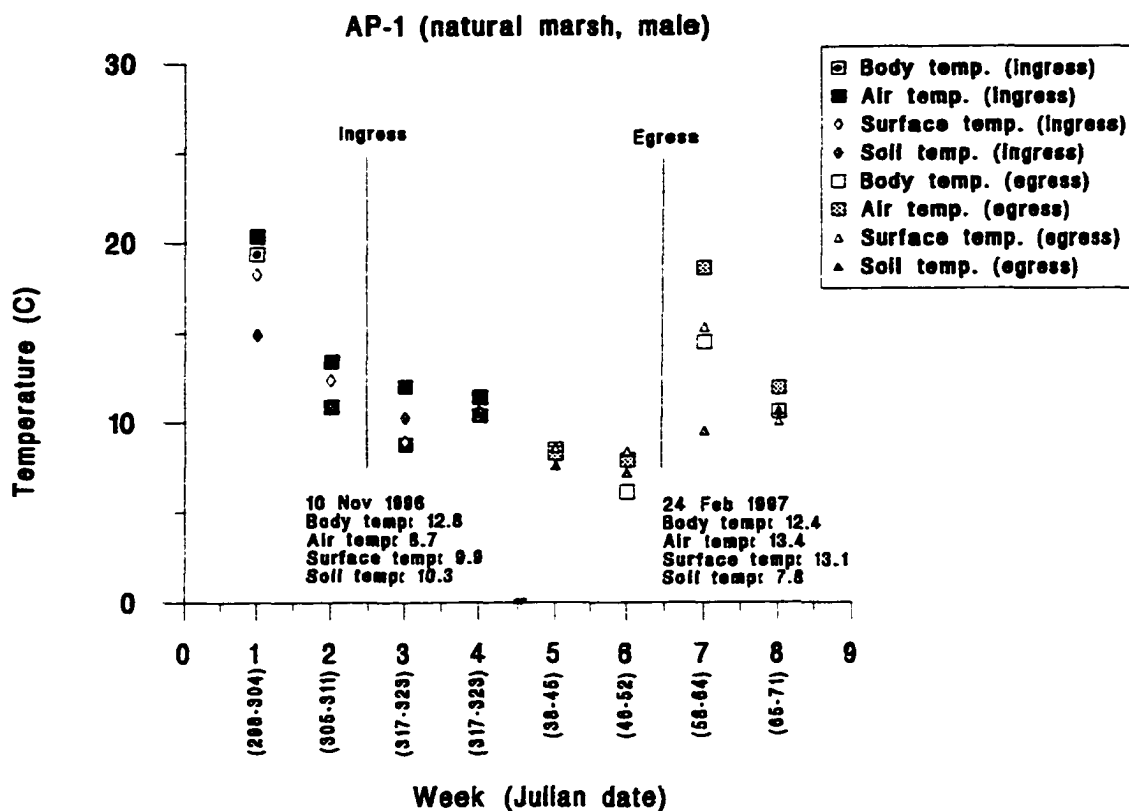


FIG. 23.—Body and environmental temperature profiles for subject AP-1 (natural marsh, male) at Back Bay National Wildlife Refuge. Profiles show weekly mean temperatures for eight weeks—two weeks prior to and after ingress into the hibernaculum, and two weeks prior to and after egress from the hibernaculum. Ingress and egress dates, as well as body, air, surface, and soil temperatures for ingress and egress dates are shown.

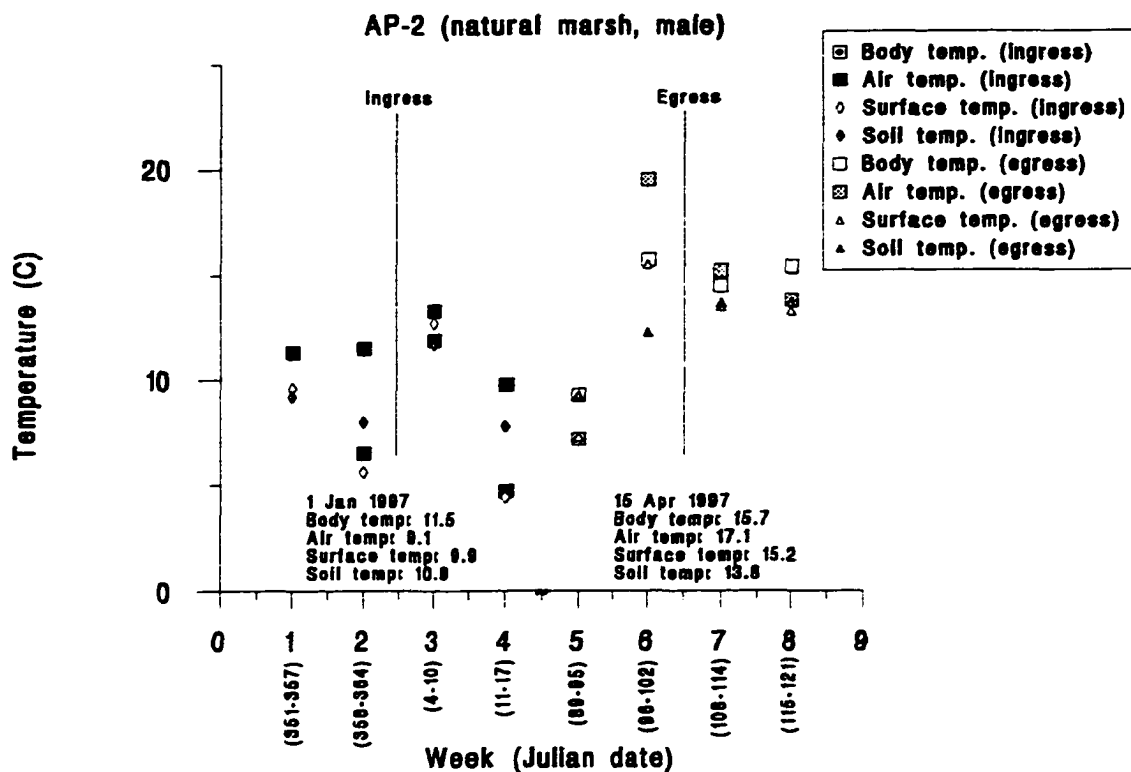


FIG. 24.--Body and environmental temperature profiles for subject AP-2 (natural marsh, male) at Back Bay National Wildlife Refuge. Profiles show weekly mean temperatures for eight weeks--two weeks prior to and after ingress into the hibernaculum, and two weeks prior to and after egress from the hibernaculum. Ingress and egress dates, as well as body, air, surface, and soil temperatures for ingress and egress dates are shown.

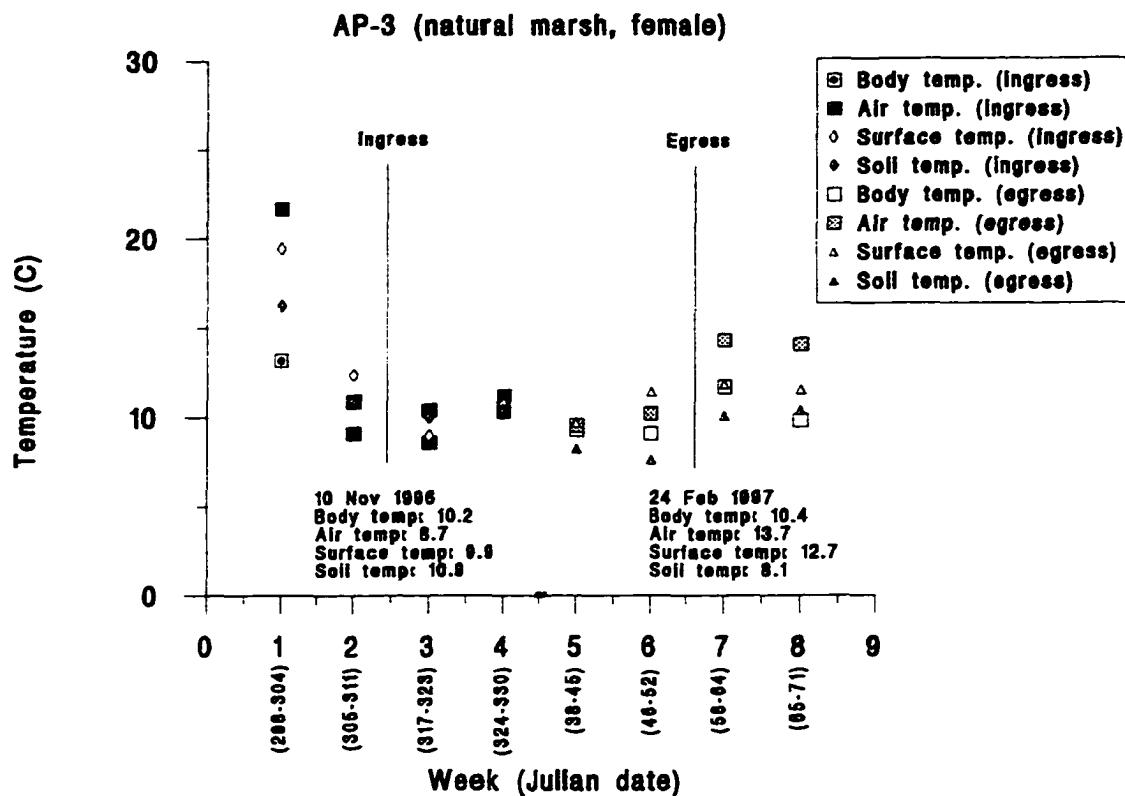


FIG. 25.—Body and environmental temperature profiles for subject AP-3 (natural marsh, female) at Back Bay National Wildlife Refuge. Profiles show weekly mean temperatures for eight weeks—two weeks prior to and after ingress into the hibernaculum, and two weeks prior to and after egress from the hibernaculum. Ingress and egress dates, as well as body, air, surface, and soil temperatures for ingress and egress dates are shown.

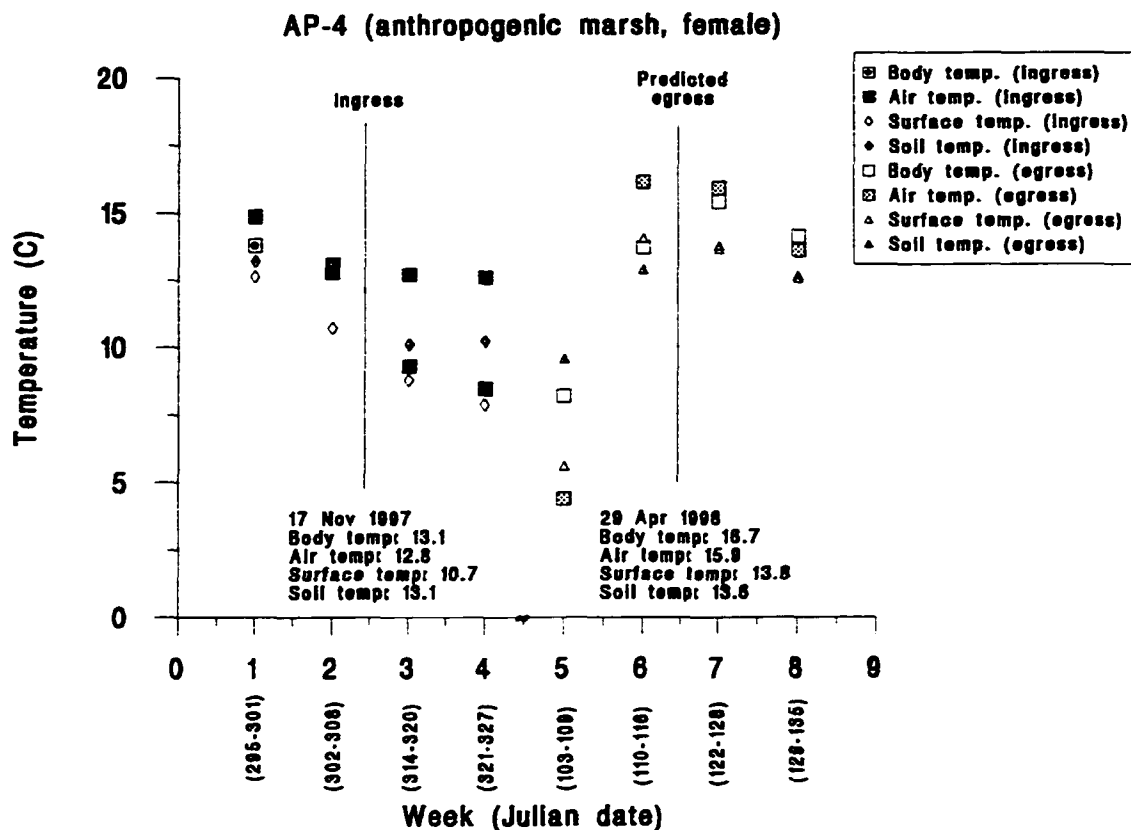


FIG. 26.--Body and environmental temperature profiles for subject AP-4 (anthropogenic marsh, female) at Back Bay National Wildlife Refuge. Profiles show weekly mean temperatures for eight weeks--two weeks prior to and after ingress into the hibernaculum, and two weeks prior to and after egress from the hibernaculum. Ingress and egress dates, as well as body, air, surface, and soil temperatures for ingress and egress dates are shown.

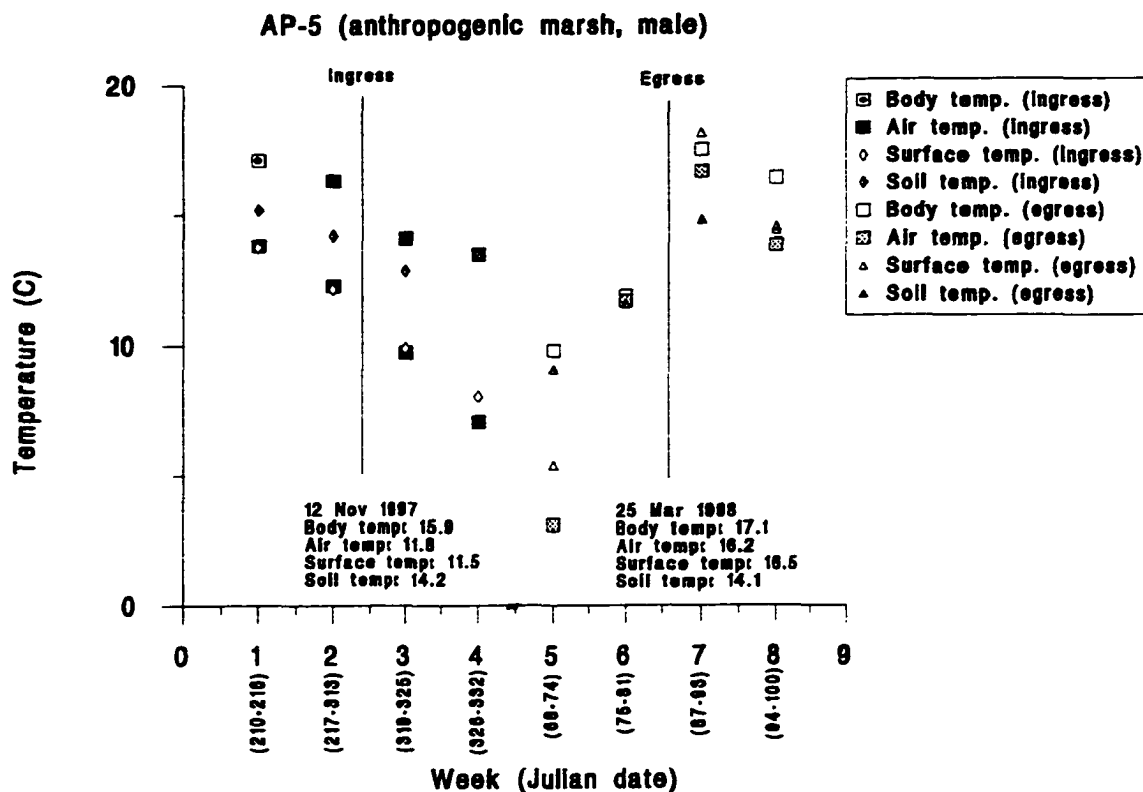


FIG. 27.--Body and environmental temperature profiles for subject AP-5 (anthropogenic marsh, male) at Back Bay National Wildlife Refuge. Profiles show weekly mean temperatures for eight weeks--two weeks prior to and after ingress into the hibernaculum, and two weeks prior to and after egress from the hibernaculum. Ingress and egress dates, as well as body, air, surface, and soil temperatures for ingress and egress dates are shown.

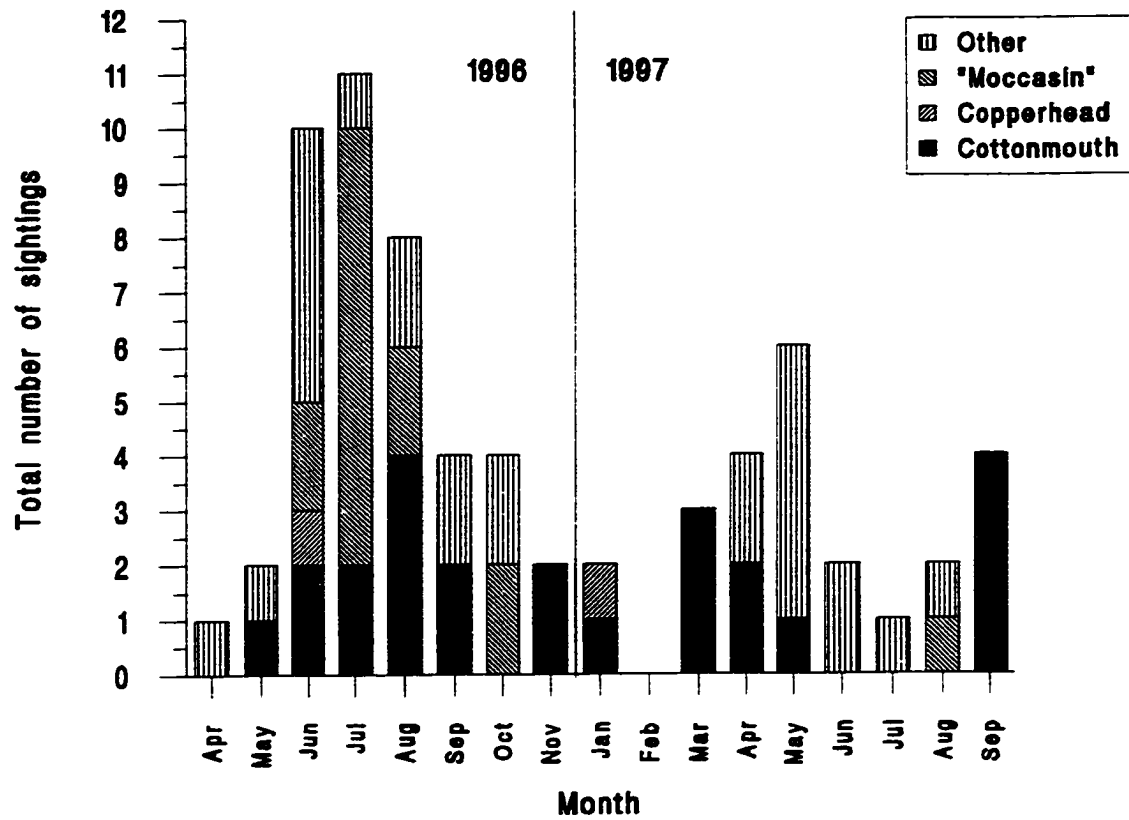


FIG. 28.--Snake sightings by visitors at Back Bay National Wildlife Refuge during 1996 and 1997. The categories shown include copperheads, a species reported quite often at the Refuge, but which does not occur there.

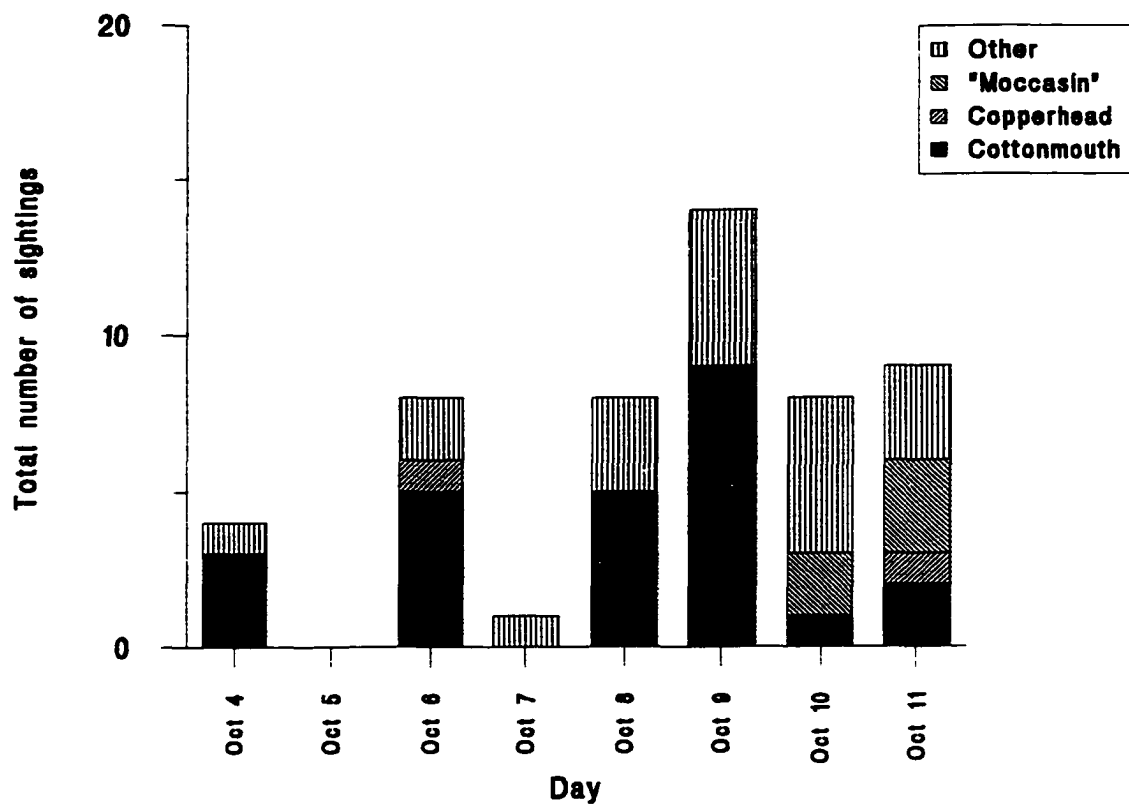


FIG. 29.—Snake sightings by hunters at Back Bay National Wildlife Refuge during 1997. The categories shown include copperheads, a species reported quite often at the Refuge, but which does not occur there.

DISCUSSION

Ecological Analysis

Morphological comparisons did not differ between the natural and anthropogenic marsh habitats in any of the categories examined in this study, suggesting that the two habitats, although quite different in visual appearance, offer similar requirements necessary for growth and survival. Blem and Blem (1995) reported that the cottonmouths from Hopewell, Virginia and the 51 males and 25 females they examined from southeastern Virginia and northeastern North Carolina differed with respect to SVL, tail length / SVL, head length / SVL, and head width / SVL. However, 41 of their specimens from southeastern Virginia and northeastern North Carolina were from museum collections. Animals gathered for such collections may be the largest, and hence most conspicuous individuals, which may lead to differences not seen in wild populations.

Growth is difficult to assess in snakes unless the age at initial capture is known. In most mark-recapture studies involving snakes, all snakes encountered are captured, and therefore age at initial capture is unknown. Using a large database of size and age categories for *Opheodrys aestivus*, Plummer (1997) was able to assign ages to captured snakes. This allowed him to use the Von Bertalanffy growth model to predict growth rate as a decreasing linear function of length. This type of information, however, is not available for cottonmouths, although Blem and Blem (1995) provide conservative estimates relating length and age for cottonmouths in their northernmost location. Since this information was not available for the BBNWR populations, differences in morphological measurements for snakes recaptured one year after initial capture were examined. Growth was seen in nearly all size categories for both sexes, with the greatest growth observed in SVL for male snakes. This suggests that the cottonmouths at

BBNWR are healthy and that food is available in quantities great enough for growth to occur.

Blem (1981) reported that 83% of the females from his Hopewell, Virginia population were gravid. He concluded that cottonmouths in that population reproduce on an annual cycle. Later, Blem (1982) suggested that this high ratio may have been the result of the size of the females in the population, because variation in the proportion of reproductive females is likely a function of size of the females, since lipid reserves necessary for reproductive output are greatest in larger females. Based on the results of his study, which found that approximately 70% of females in the SVL size class 600–750 mm were gravid, I expected that a much higher percentage of females at BBNWR would have been gravid, given their average SVL of approximately 625 mm in both marshes. However, less than 25% of the captured females were gravid in either year in either marsh. Perhaps this is the result of gravid females at BBNWR seeking densely vegetated basking areas, where they are quite inconspicuous.

Cottonmouths are known to be highly aquatic, spending the vast majority of their time along shorelines (Wharton, 1969; Gloyd and Conant, 1990; Mitchell, 1994; Blem and Blem, 1995). In this study, most cottonmouths were categorized as occupying upland areas regardless of sex, type of marsh, or whether they were a capture-recapture or radiotelemetry subject. Snakes in this category, however, included any distance > 0.5 m from water. Most snakes were found less than 1.5 m from a water source throughout the study, suggesting that a nearby water source is important for cottonmouths at BBNWR. Perhaps more use-categories may better describe shoreline habitat use by cottonmouths.

Living vegetation was the most common source of cover in both marshes, though most animals were found fully exposed to the sun. Given that the majority of both of these habitats is covered by marsh plants, it is not surprising that the snakes chose vegetation as cover. However, it was surprising that most snakes remained in full sun and

that those close to areas of high tree density did not seek those areas for shade during the hottest part of the day.

The position of the snakes when found was nearly always stationary, either extended or coiled; only a few snakes were found moving. Radiotelemetry subjects were found in tight coils much more often than were mark-recapture animals in either marsh. Mark-recapture animals may have sensed my approach well before I was close enough to spot them, and the extended position in which they were found may indicate that they were getting into a position from which it was much easier to flee (i.e., extended as opposed to coiled), or that they were fleeing and stopped upon my approach. Alternatively, extended animals may have been more readily visible, and hence the majority of coiled animals that were seen were those that were implanted. Blem and Blem (1995) reported that the snakes that they captured in Hopewell, Virginia were almost always found coiled, and Wharton (1969) found most of his animals tightly coiled on hot days. The behavioral difference between the two studies and between radiotelemetry and mark-recapture is unclear; however, radiotelemetry specimens may have simply been displaying coiling behavior as a result of the surgical implantation of radiotransmitters, or I may have approached the radiotelemetric subjects more cautiously, thereby causing less disturbance, and hence the snakes remained coiled.

Contrary to anecdotal accounts of cottonmouths displaying aggressive behaviors and even charging potential threats (e.g., humans), few snakes reacted more aggressively than a simple gape of the mouth and vibration of the tail against the substrate, indicating that the cottonmouths in this study were much more apt simply to make their presence known than to aggressively react against human invasion of their activity ranges. No snakes attempted to flee at temperatures $< 18^{\circ}\text{C}$, in accordance with the temperature correlations reported by Wharton (1969); however, aggressive behaviors occurred at all temperatures. Only on two occasions throughout this investigation did snakes approach the investigator in an aggressive manner; both were very large males. The snakes gaped

their mouths, swam to within 2 m of the investigator, rapidly vibrated the tail against the water surface, and struck repeatedly. After approximately 1-2 minutes, the snakes turned to flee before being captured. A similar account was reported by Neill (1947) for a cottonmouth in Georgia.

The majority of the 53 uncaptured snakes in this investigation fled before the investigator was within capture distance. On two occasions snakes fled by diving underwater between the investigator's legs. These snakes displayed no aggressive behavior and were likely fleeing to the closest source of water. Snakes in the anthropogenic marsh fled at a greater approach distance than those in the natural marsh, but the difference was not statistically significant. The snakes in the anthropogenic marsh may be more aware and hence reactive to potential threats given their greater exposure to large, predatory wading birds, carnivorous mammals, machinery used in pool management, and hikers along the dike trails. Snakes in the natural marsh are generally free of such potential hazards, with the exception of a few predatory wading birds and hikers. The medium to which a snake fled (land or water) was not affected by the medium from which it was approached or the medium that the snake was in, suggesting that the snakes simply fled opposite to the direction of approach.

Habitat Analysis

Accurate measurements of an animal's habitat and an understanding of the relationship between habitat availability and use by an organism are invaluable for conservation and management efforts (Carey, 1981; Morrison et al., 1992). The increased use of radiotelemetric techniques has led to a better understanding of habitat use by snakes (Reinert, 1984a, b, 1992, 1993), but the evaluation and statistical treatment of the data obtained from such studies continues to be problematic (North and Reynolds, 1996). The data gathered in this study for both mark-recapture and radiotelemetry subjects allowed

for the application of traditional modeling techniques (use vs. non-use sites; Reinert 1984a, b) and logistic regression techniques (North and Reynolds, 1996).

A MANOVA on ranked data was used to compare the 11 habitat variables measured for each of 11 categories: random sites in both marshes, males and females in both marshes, and five radiotracked animals. Random sites within the natural and anthropogenic marshes differed with respect to several variables: distance to nearest overstory tree was greater in the anthropogenic marsh, distance to understory tree was greater in the anthropogenic marsh, percent canopy closure was greater in the natural marsh, percent leaf cover was greater in the natural marsh, and stem height was greater in the natural marsh. These results directly follow from the management activities that occur in the anthropogenic marsh at BBNWR. Large areas of the anthropogenic marsh are mowed and root raked, and trees are removed, resulting in lower stem height, greater distances to trees, less accumulation of leaf litter, and reduced canopy closure.

Mark-recapture snakes were found in close proximity to water for all categories, as were snakes AP-3 and AP-4. Snakes AP-1, AP-4, and AP-5 were found far from water sources. However, since these snakes moved to upland areas prior to hibernation, the average distance to water is biased; removal of location data immediately pre-hibernation and post-hibernation reduces this disparity. On the other hand, since searches for mark-recapture animals generally took place close to water sources, the distance to water may be biased low for these animals. However, searches for animals did occasionally take place in more upland areas, but no snakes were found.

Discriminant function analysis (DFA) for habitat use analyses is often plagued with the problem of unsatisfactorily fulfilling the requirements necessary for unbiased results, namely multivariate normality and a constant covariance structure. To get around these restrictive assumptions, a rank transformation was performed on the data, making it equivalent to a nonparametric procedure. Performing both the traditional method and the logistic regression method made it possible to compare the two statistical techniques. The

DFA worked well for these data, as evidenced by a high percentage (> 90%) of the observations correctly classified by crossvalidation reclassification. Canonical correlations generated by the analysis indicated that diameter at breast height of the nearest understory tree, distance to the nearest understory tree, distance to water, percent of leaf cover, percent vegetation cover, and percent canopy cover all were important for differentiating use versus non-use sites.

Polytomous logistic regression (PLR) was used to evaluate habitat use from radiotelemetric data. PLR does not require assumptions about normality, nor does it require a constant covariance structure across use categories (North and Reynolds, 1996). Choosing grid-cell size is, however, problematic. PLR was developed for habitat analysis by North and Reynolds (1996) as a way to delineate foraging microhabitat for the northern spotted owl (*Strix occidentalis caurina*). Specific forest stands were used in their analysis rather than grid cells because specific stands could be identified as foraging areas. I developed the use of grid cells for PLR habitat analysis for a re-analysis of the *Agkistrodon contortrix* data of Petersen (1995; Cross, unpublished) because snakes presumably could potentially use any area within the macrohabitat in which they are found. Grid cell size was chosen based on the mean distance moved per day. In this study, subject AP-2 was not used in this calculation given the exceptionally long movements that occurred for the first two weeks after transmitter implantation. The mean movement for AP-1 and AP-3 through AP-5 was 12.01 m, and therefore the grid cells were chosen to be 12.5 m on each side. In this way, snakes could potentially be in a different grid cell on any given day.

The assignment of use categories to the data also can be problematic. In the current study the use categories were assigned after plotting and examining grid cell usage patterns for the five radiotracked snakes. Three divisions (low, medium, and high use) were obvious from the data, but more or less than three divisions could be possible given additional data. The variables that delineated the use-categories were: distance to water,

distance to understory tree, leaf litter cover, and percent vegetation cover. Snakes in high use categories were generally found farther from water, closer to understory trees, and in areas of relatively higher canopy closure and leaf litter than the lesser used areas. All four of these variables were also chosen by the DFA procedure, perhaps indicating that both DFA and PLR worked well with these particular data. Unfortunately habitat data from other areas where the cottonmouth occurs have not been collected and analyzed in an equivalent manner. However, the data indicate that the BBNWR cottonmouths are found in association with the classical habitat factors found in marsh systems, namely water, vegetation, and small wetland trees, and not in adjacent, upland forested areas (unless hibernating).

The use of PLR for modeling snake microhabitat seems to be a useful technique and does not require the often unobtainable assumptions of DFA or other multivariate techniques. Additionally, PLR does not require the time-consuming task of collecting ancillary data from "non-use" animal sites. This is an important consideration because there is no *a priori* reason to believe that the microhabitat characters gathered from a random selection of sites is in any way indicative of a site that would be avoided by an animal, particularly if the random site falls within the activity range of the study organism (North and Reynolds, 1996).

The use of radiotelemetry locations for PLR modeling, while not requiring the use of absence sites, still does not solve all of the problems of microhabitat analysis (North and Reynolds, 1996). Radiotelemetry location analysis makes the assumption that the snake is at a chosen site when located and that the percentage of use of a given site reflects the inherent microhabitat value of the location. Further, assigning a use category to sites assumes that all sites within an assigned category have equal importance to the organism (North and Reynolds, 1996). In reality, however, it may be that the most important sites are visited by the snakes when it is not being tracked. That is, if an animal is spending only a small fraction of its time in a highly important area, then the animal may never be at

the key area when located, and hence the microhabitat variables associated with that area may never be included in the sample. Given the tracking frequency in this study, however, this is likely not a limitation in this study.

Population Estimation

Estimates of population size were relatively high at BBNWR, but the confidence intervals around the point estimates were generally wide, a result of having few recaptures. The population estimate for the natural marsh dropped dramatically in 1997, but the number of recaptures in that marsh also increased, resulting in a narrowing of the confidence interval. This suggests that the population estimates for the marshes may be slightly inflated as a result of few recaptures, which was expected given the sensitivity of the Schnabel method to recaptures (Seber, 1982). However, having few recaptures may also mean that a very small percentage of the population was captured throughout the study, which could bias the point estimates negatively. Clearly additional estimation methods are needed for this type of work (Seber, 1992).

Population size estimates did not differ significantly between the marshes. Wharton (1969) estimated cottonmouth densities to be as high as 9.02 snakes/ha on Sea Horse Key, Florida; however, that study was conducted on an island. Snakes from a mainland population occurred in densities of 0.75 snakes/ha. Blem and Blem (1995) estimated densities in Hopewell, Virginia to be <0.01 snakes/ha. BBNWR populations were intermediate between those above, ranging from 0.13-0.26 snakes/ha for both marshes. Linear densities for cottonmouths are not generally reported, but Blem and Blem (1995) reported "locally high" densities of only 0.0025-0.005 snakes/m. Snakes from BBNWR had a linear density of 0.02-0.05 snakes/m, meaning that, on average, a snake might occur in every 20-50 m of shoreline investigated. Like the population estimate from which it is derived, the estimated density is likely to be positively biased

given that it is derived from population estimates that were positively biased. However, BBNWR clearly has relatively high densities of cottonmouths in both the natural and anthropogenic marsh habitats.

Sex ratios for field-collected cottonmouths were male-biased in both marshes in both years. Blem and Blem (1995) reported similar results for both their northern Virginia and southeastern Virginia/northeastern North Carolina populations. They also noted that 93 cottonmouths born in captivity were not sex-biased (45 females and 48 males). This suggests that either males are more likely to survive in the wild, or that males are more active and hence are captured in greater numbers than females because they are more conspicuous. The latter is the most likely scenario, but this was not tested in this or other studies.

Foraging and Feeding Ecology

Most of the stomachs examined in this study contained some type of food material, usually an unidentifiable slurry. Many field studies report very low percentages of snakes with gut contents (Barbour, 1956; Wharton, 1969; Collins and Carpenter, 1970; Blem and Blem, 1995).

Cottonmouths often eat other snakes, including their own kind (Wharton, 1969; Blem and Blem, 1995), and the remains of a *Nerodia sipedon* were found in one of the stomachs examined in this study. Many *N. sipedon* were seen in the management pools in the anthropogenic marsh, particularly in the younger pools, but no guts of cottonmouths in the anthropogenic marsh contained snakes.

The majority of the stomachs examined contained the remains of fish and frogs. Electroshocking surveys conducted by U. S. Fish and Wildlife Service fishery biologists suggest that fish are abundant in the management pools, but that densities in Back Bay are low. Therefore, it was postulated that snakes in the anthropogenic marsh might prey on

fish more often than those in the natural marsh. However, the roadside ditches in the natural marsh, which were not surveyed for fishes, contained many sunfishes (*Lepomis* spp.). Seventy-five percent of the fishes obtained by palping stomachs were from snakes in the natural marsh, contrary to the hypothesis. Frogs were found in high numbers at BBNWR in both the natural and anthropogenic marsh habitats (estimated 2.1 frogs/m² in some locations), and they made up a large proportion of the prey consumed by cottonmouths in both marshes. Active foraging in water, presumably for frogs and fish, was observed in both marshes, and the swallowing of a still-living frog was seen in the natural marsh.

Radiotelemetry

Movements of cottonmouths were variable between marshes and between sexes. The largest total distances moved were by males AP-2, in the natural marsh, and AP-5, in the anthropogenic marsh. Male AP-2 made an extraordinarily long movement of approximately 640 m in a 24-hour period, but moved relatively little after that. Male AP-5 moved almost twice the total distance of AP-2, but did so in a series of east-west movements in a ditch as opposed to a large single movement. Females moved less on average than did males, a trend also seen by Petersen (1995) for *Agkistrodon contortrix* (see also Brown et al., 1982 and Reinert and Zappalorti, 1988 for *Crotalus horridus*). The snakes in the anthropogenic marsh moved farther on average than did those in the natural marsh. The ditches surrounding the management impoundments in that marsh served as a direct means of long-distance movements, perhaps explaining the relatively large mean distances per movement for these snakes.

Activity ranges calculated by both the minimum convex polygon (MCP) method and the harmonic mean method (95% isopleth) were similar, with the exception of the area calculated for AP-2. The difference in these measures for this snake is attributable to the

shape of its activity range as constructed by the harmonic mean method, which included large areas on the southern end of the activity range that were not used by the snake. Perhaps this snake had been pushed south by wind-driven currents on Back Bay (it was located immediately after exiting the water), and therefore moved farther in an attempt to return to its previous location. The activity range for this snake should be interpreted cautiously. The remainder of the snakes had MCP activity ranges of 0.48 ha-54.54 ha. These activity ranges were similar to those of the congeneric *Agkistrodon contortrix* studied by radiotelemetry in southeastern Virginia (Petersen, 1995). Mark-recapture subjects had activity ranges that were comparable to radiotracked snakes, with males using larger areas ($\bar{x} = 2.98$ ha) than females ($\bar{x} = 1.74$ ha). Wharton (1969) found that the mean activity ranges of his snakes, determined by mark-recapture sampling, were 0.142 ha for females and 0.174 ha for males and that they were the approximately the same for both the mainland and island snakes. Range lengths (100-1700 m) for mark-recapture snakes were comparable for the current study and Wharton's (1969) study.

Snakes emerging from hibernation characteristically made long initial movements followed by a roughly two-week period of little to no movement. It was during this time that the snakes sloughed their skin. Reinert (1993) suggested that this reduction in movement prior to shedding events may reduce predation risk for snakes with opaque skin covering the eyes. Petersen (1995) found the same pattern of reduced movement prior to shedding events in his study of *Agkistrodon contortrix*.

Snakes have been suggested to exhibit learned behavior (or use of persistent cues over time), as evidenced by the repeated use of the same sites over time. This has been demonstrated, for example, for the pitvipers *Agkistrodon contortrix* (Petersen, 1995), *Crotalus h. horridus* (Reinert and Zappalorti, 1998), and *Crotalus h. atricaudatus* (A. H. Savitzky, *personal communication*). In the current study, I removed two large male cottonmouths from the edge of the educational pond at BBNWR to prevent interactions with humans. Both snakes were translocated approximately 500 m away, in opposite

directions. Within 72 hours both snakes had returned to the location from which they had been initially removed. The snakes were again moved the same distance, but to different locations than they had been previously. Neither snake returned to the removal location. It is not clear whether the snakes did not return due to continued harrassment by the investigator or whether they were moved outside of their activity ranges and hence were unable to orient back to the original location.

Biweekly mean movements for the cottonmouths in this study showed relatively large autumnal movements, followed by a period of reduced movement before hibernation. Biweekly means for spring movements showed long-distance movements immediately following emergence from hibernacula (as noted above), followed by a series of shorter movements. Data were inconclusive in terms of increased male movement during late spring, as would be expected for snakes that seek mates at that time. Mark-recapture data do indicate increased activity of males during spring, however.

Snake body temperatures were highly correlated with air, surface, and soil temperatures during the active season, as expected given the relatively high and stable environmental temperatures associated with southeastern Virginia during the active season of these snakes. During hibernation, body temperature would be predicted to be most highly correlated with soil temperature if snakes overwinter in underground hibernacula, and most highly correlated with air or surface temperature if they do not hibernate or if they seek shallow temporary shelters during the coldest months. This pattern was seen in the current study. That is, body temperature was most highly correlated with soil temperature for AP-1, AP-3, AP-4, and AP-5, all of which hibernated underground. Snake AP-2, which spent the coldest months under dense vegetation but above ground, had a body temperature most highly correlated with air temperature.

All snakes that hibernated underground went into root tunnels after a drop in air and surface temperatures of approximately one month, when soil temperature was beginning to remain consistently higher than air temperature. Surprisingly, this is the same

pattern observed for AP-2. This snake ceased movement and went under dense vegetation under a similar temperature regime. Emergence followed the opposite pattern, wherein a one-month increase in air and surface temperature seemed to trigger emergence. Both female snakes moved to new hibernacula during the winter, and AP-3 moved back to her original location approximately two weeks later. AP-4 only moved approximately 1.5 m, but died before emerging. Her hibernaculum was inundated during an unusually wet winter. It is unclear why AP-3 moved.

Selection of hibernacula over time was not examined in this study, but the choice of upland hibernacula quite distant from active season movements in the anthropogenic marsh and the movement of females to new hibernacula suggest that the snakes may use ancestral chemical cues to find adequate hibernacula within their activity ranges. Long distance movements to hibernacula have been discussed by Gibbons and Semlitsch (1987). Use of the same hibernacula over time has been demonstrated for the two other pitvipers in southeastern Virginia, *Agkistrodon contortrix* (Petersen, 1995) and *Crotalus horridus atricaudatus* (A. H. Savitzky, personal communication).

Sexton et al. (1992) predicted that snakes south of 38° latitude should hibernate solitarily, use temporary cover, or be active all winter, whereas those above 38° latitude should hibernate communally. Snakes AP-1 and AP-3, along with at least two other non-telemetered individuals, shared the same hibernaculum, whereas AP-4 and AP-5 used solitary hibernacula, and AP-2 used temporary cover. This mix of hibernation behaviors might be expected given the borderline latitude of southeastern Virginia (36°). Wharton (1969), on the other hand, found that his Florida cottonmouths hibernated communally in rotting stumps. This may be attributable to adequate hibernacula being a limiting resource on the island in which Wharton (1969) worked. Hibernacula do not appear to be limited at BBNWR in either marsh habitat.

Sightings by Visitors and Hunters

Many snakes were reported by visitors to BBNWR, although the number reported is negatively biased because many visitors do not record their sightings in the Refuge log book. Nonetheless, many more snakes were reported in 1996 than in 1997, although it is unclear why. As many as 14 snakes were seen on a single day during October 1997 by hunters, but not a single report was made by a visitor for that same period. Since hunters were in areas closed to hikers, it was expected that they would see more snakes. Many of the hiking trails, however, border marsh areas where snakes can be seen almost daily, thereby making it difficult to believe that no snakes were seen by visitors. An effort must be made to convince Refuge visitors to record animals that they see in order for proper management strategies to be employed.

Copperheads (*Agkistrodon contortrix*) are found in nearly every county in Virginia, though they have never been found at BBNWR. Interestingly, Pague and Mitchell (1991) list the copperhead as occurring on the barrier beach area of BBNWR, but not on the Pungo Ridge area on the western side of Back Bay proper, where it is known to occur (Linzey and Clifford, 1981; Mitchell, 1994). Given the similar appearance of juvenile copperheads and cottonmouths (Gloyd and Conant, 1990), the copperheads reported at BBNWR were probably misidentified cottonmouths.

Management Strategies

Management strategies for pitvipers are not commonly constructed or implemented, perhaps a result of the negative attitudes associated with the preservation of venomous reptiles. A recent study by Johnson and Leopold (1998) on the eastern massasauga (*Sistrurus c. catenatus*) suggested management strategies to sustain and

perhaps increase the numbers of massasaugas in New York. The massasauga is endangered in New York and was found in very low densities on their research site. Management plans need not only be implemented for endangered species or for species that are overabundant (e.g., *Odocoileus virginianus* in many states). Conservation efforts for populations at presumably reasonable densities should be examined, particularly in areas where management of other species is given priority.

Cottonmouths are a dominant carnivore at BBNWR, occurring in large numbers. The Back Bay National Wildlife Refuge Station Management Plan (BBNWRSMP; Station Management Plan: Back Bay National Wildlife Refuge, July 1993) does not mention cottonmouths in the discussion of wildlife resources at the Refuge nor in the 28 management objectives in the BBNWRSMP. The Refuge is dedicated to the management of waterfowl and shorebirds and does spend resources on the management of nontarget species, such as migratory songbirds, white-tailed deer, and nutria (*Myocastor coypu*), an introduced species. The lack of management for the cottonmouth likely reflects inadequate time, money, and understanding of this animal, however, rather than disdain for the species. I suggest that the managers of BBNWR study both this report and the field methodologies of Jones (1986) to obtain a better understanding of the reptiles at the Refuge and how they fit into the BBNWRSMP.

Both the natural and anthropogenic marshes at BBNWR support large numbers of *Agkistrodon piscivorus*. I initially expected that the natural marsh would support more individuals given the large-scale disturbances (such as mowing and burning) that occur in the anthropogenic marsh. This does not seem to be the case, however. Management of water level, root-raking, plowing, and burning of large sections of the management impoundments does result in the temporary local displacement of cottonmouths from those areas, but the cottonmouths likely move to undisturbed areas within the anthropogenic marsh system until conditions are suitable for their return. Food resources

for cottonmouths are presumed not to be limited, and therefore snakes can move to new areas without having to deal with limited prey availability.

Johnson and Leopold (1998) suggested that clearing and burning in the wetlands where they studied the eastern massasauga might offer more basking areas, and hence increase snake numbers. Cottonmouths, on the other hand, use areas of fairly high vegetation cover even when areas of early successional, low-density vegetation are available. This result is presumably related to the use of shoreline and water bodies by the cottonmouth. The areas surrounding drainage ditches and areas with fairly deep water all year have comparatively high vegetation cover. These are the areas where cottonmouths are most often found. The anthropogenic marsh habitat is bordered on the east by unmanaged "fingers" of marsh habitat that extend into Back Bay proper. These areas are occasionally used by cottonmouths, but do not seem to offer refuge after intense manipulations of the impoundments are performed. Apparently the snakes find adequate cover simply by moving to different areas within the management impoundments. Management in the anthropogenic marsh should focus on leaving adequate cover for the cottonmouth near areas of impoundment manipulations. Manipulations of entire management pools would likely result in reduced numbers of cottonmouths. Both Wharton (1966) and Blem and Blem (1995) suggest that continued disturbances of cottonmouths leads to permanent local extirpation of populations. It is not clear what long-term effects manipulations of impoundments would have on cottonmouth populations at BBNWR.

Disturbances in the natural marsh are rare, and common sightings of cottonmouths by visitors in that area are generally limited to marsh areas along footpaths and in drainage ditches along the road. Many snakes in the natural marsh are out of sight of visitors and therefore enjoy the protection granted by dense marsh vegetation and low shrubs. Management of the natural marsh, therefore, should simply include strategies to leave the area undisturbed.

Cottonmouths occasionally are eaten by carnivorous mammals (foxes and raccoons), large wading birds (herons and egrets), and even ghost crabs (*Ocypode quadrata*; Cross and Marshall, 1998). Predation pressure on cottonmouths at BBNWR is unknown, but it is thought that most predation is limited to juveniles, because adults are much larger and hence more dangerous to predators than juveniles. Management should focus on leaving adequate habitat for cottonmouths so they can forage effectively, find shelter, and reproduce in numbers great enough to counterbalance the effects of juvenile mortality.

A survey of presumably adequate hibernation areas demonstrated that hibernacula do not seem to be limited at BBNWR. The cottonmouths studied either spent winters in underground root tunnels or under dense vegetation in the natural marsh, and in root tunnels in upland areas of the anthropogenic marsh. The greatest threat to overwintering cottonmouths at BBNWR would likely be the further destruction of areas where adequate hibernacula can be found. If the natural marsh is left undisturbed, hibernacula should remain an unlimited resource. In the anthropogenic marsh, however, conversion of the forested area ("green hills area") to management impoundments could be disastrous for cottonmouth populations and might lead to their rapid decline and eventual extirpation from the anthropogenic system. It is therefore strongly suggested that the higher, forested wetlands on the eastern side of the management impoundments be left intact.

FINDINGS AND INTERPRETATIONS

1. Morphological measurements did not differ between cottonmouths in the natural and anthropogenic marsh habitats. This lack of location effect suggests that cottonmouths have the required resources available for growth and survival in both marsh systems, and that they are perhaps the same population.
2. Growth was difficult to assess in the current study given the low number of recaptures over time. Several snakes were recaptured approximately one year after initial capture, however, and provided information on growth. Snakes of both sexes and in both marshes grew in all morphological categories except tail length and mass. It is not known whether the lack of mass gain was due to handling or simply because the snakes did not feed close to the capture date.
3. Most snakes were found > 0.5 m from water. Live vegetation served as the primary cover object for cottonmouths, but many were found in the open and in water. Most snakes were found with the body extended and in direct sunlight regardless of temperature. Nearly all snakes remained in place upon approach, but several also fled before capture. Snakes fled in the direction opposite the investigator no matter which medium (land or water) they occupied at the time. Snakes that behaved aggressively usually did so after they were disturbed with tongs. Aggressive behavior was rare upon approach of most snakes.
4. Males were captured more frequently than females in both natural and anthropogenic marshes, likely a result of male snakes being more active and thus more conspicuous. Few females were gravid in either marsh, suggesting that cottonmouths at BBNWR do not reproduce annually or that gravid females are not as catchable.

5. A MANOVA of eleven habitat variables revealed several differences between males and females, between snakes in the natural and anthropogenic marsh habitats, and between mark-recapture and radiotelemetered subjects. Discriminant Function Analysis (DFA) and Polytomous Logistic Regression (PLR) both suggested that the most important habitat variables for determining sites used by cottonmouths in both marshes were: distance to water, distance to understory trees, leaf litter cover, and vegetation cover. Though habitat structure differed between the natural and anthropogenic habitats, snakes apparently occupy both habitats because both provide adequate cover and access to foraging areas.
6. PLR provided an effective means of elucidating important habitat variables based on use-only sites. Unlike DFA, non-use sites were not necessary for assessing important habitat variables, thereby eliminating assumptions about random locations. Since both DFA and PLR provided similar results in this study, I suggest that further work be performed to compare these methodologies and to assess the effects of grid size on PLR analyses.
7. Population sizes and relative densities for cottonmouths were high for both the natural and anthropogenic marsh systems at BBNWR and were higher than for the northern population of cottonmouths in Virginia.
8. Estimation of population size by a modified Schnabel Census methodology provided adequate estimates from the mark-recapture data gathered during this study. Confidence intervals were quite large for some estimates, suggesting that the low number of recaptures, a common problem with snake studies, may lead to biased estimates of population size. Areal density estimates were within the range of many

other studies of snake populations, but given the heavy use of limited areas of both marshes (e.g., around water bodies), areal densities were considered unreliable. Linear density, a measure of the number of snakes per linear meter (hence not a true density estimate), was deemed more reliable for this study. Linear densities were quite high for both the natural and anthropogenic marshes, and were much higher than for the other population in Virginia.

9. Unlike many other studies of cottonmouths, the majority of stomachs sampled in this study contained food items. Snakes in both marshes fed primarily on frogs and fish, consistent with the high densities of these prey animals in both marsh habitats. Many stomachs contained inedible items (sticks, rocks, etc.). This has been reported elsewhere and is likely the result of incidental ingestion.
10. Activity ranges of radiotracked snakes were quite variable in this study. Snakes in the anthropogenic marsh had, on average, larger activity range areas than snakes in the natural marsh. This may be due to the ease of movement along dredged ditches in the anthropogenic marsh. Activity ranges for mark-recapture cottonmouths estimated by geometric methods fell within the range of areas estimated for radiotelemetered snakes. Mark-recapture males had larger activity areas than did females.
11. Snake body temperature was highly correlated with air, surface, and soil temperatures during the active season, but was usually most highly correlated with soil temperature during hibernation. One snake did not seek an underground hibernaculum, but rather spent the coldest months under dense vegetation. The body temperature of this snake was most highly correlated with the air and surface temperature.

12. Snakes entered hibernacula or sought cover after a four week decline in average air and surface temperatures, and when air and surface temperatures fell below average soil temperature. Snakes emerged from hibernation after approximately four weeks of increasing air and surface temperature. Surveys suggested that hibernacula do not appear to be limiting in either marsh.
13. Cottonmouths were commonly reported from both marshes by visitors and hunters.
14. Management strategies for the cottonmouth do not currently exist at BBNWR. I suggest that the greatest concern for future populations at BBNWR is the availability of adequate cover. In the natural marsh snakes can readily find cover. The manipulations of the impoundments that occur in the anthropogenic marsh presumably force cottonmouths to emigrate until they can safely return to the manipulated area. The single greatest threat to the cottonmouth population in the anthropogenic marsh is believed to be the conversion of the forested wetland into management impoundments, thereby destroying hibernacula for overwintering snakes.

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APPENDIX I

Plant List for Back Bay National Wildlife Refuge

The list is comprised of species identified during the study, as well as those obtained from Refuge files. Additional species present or historically present in the Back Bay watershed can be found in Wright (1990).

Scientific name	Common name
<i>Acer rubrum</i>	red maple
<i>Achillea millefolium</i>	yarrow
<i>Acorus calamus</i>	sweet flag
<i>Agrostis</i> sp.	bent grass
<i>Alisma subcordatum</i>	southern water plantain
<i>Allium vineale</i>	field garlic
<i>Alnus rugosa</i>	speckled alder
<i>Alternanthera philoxeroides</i>	alligator weed
<i>Amaranthus retroflexus</i>	rough pigweed
<i>Amaranthus cannabinus</i>	water hemp
<i>Ambrosia artemisiifolia</i>	ragweed
<i>Ammannia coccinea</i>	lythrum
<i>Amorpha fruticosa</i>	indigo bush
<i>Andropogon virginicus</i>	broomsedge
<i>Antennaria neglecta</i>	false pussytoes
<i>Apocynum cannabinum</i>	Indian hemp
<i>Asclepias incarnata</i>	milkweed
<i>Aster hesperius</i>	western lined aster
<i>Aster</i> spp.	aster
<i>Aster subulatus</i>	saltmarsh aster
<i>Atriplex patula</i>	sparscale
<i>Baccharis halimifolia</i>	groundsel tree
<i>Bacopa</i> sp.	bacopa
<i>Bassia hirsutifolia</i>	bassia
<i>Berchemia scandens</i>	supple jack
<i>Bidens aristosa</i>	tickseed sunflower
<i>Bidens laevis</i>	bur marigold
<i>Bidens</i> sp.	beggar's ticks
<i>Boehmeria cylindrica</i>	false nettle
<i>Boltonia asteroides</i>	boltonia
<i>Brassica juncea</i>	Indian mustard

APPENDIX I--Continued.

Scientific name	Common name
<i>Brunnichia cirrhosa</i>	buckwheat vine
<i>Calamagrostis canadensis</i>	bluejoint
<i>Callitriche</i> sp.	water starworts
<i>Calystegia sepium</i>	hedge bindweed
<i>Campsis radicans</i>	trumpet creeper
<i>Cardamine pennsylvanica</i>	Pennsylvania bitter cress
<i>Carex</i> spp.	sedge
<i>Carex stricta</i>	tussock sedge
<i>Cassia fasciculata</i>	partridge pea
<i>Centella asiatica</i>	centella
<i>Cephalanthus occidentalis</i>	buttonbush
<i>Chelone glabra</i>	turtlehead
<i>Chenopodium album</i>	goosefoot
<i>Cicuta maculata</i>	water hemlock
<i>Cirsium vulgare</i>	bull thistle
<i>Clethra alnifolia</i>	sweet pepperbush
<i>Coreopsis</i> sp.	coreopsis
<i>Cotula coronopifolia</i>	brass buttons
<i>Crassula aquatica</i>	pygmy weed
<i>Cressa truxellensis</i>	alkali weed
<i>Crypsis nilaca</i>	prickle grass
<i>Cuscuta</i> spp.	dodder
<i>Cycloloma atriplicifolium</i>	winged pigweed
<i>Cyperus erythrorhizos</i>	red-rooted flatsedge
<i>Cyperus esculentus</i>	chufa
<i>Cyperus iria</i>	rice flatsedge
<i>Cyperus</i> spp.	sedge
<i>Decodon verticillatus</i>	swamp loosestrife
<i>Digitaria</i> spp.	crabgrass
<i>Diodia virginiana</i>	buttonweed
<i>Distichlis spicata</i>	salt grass
<i>Drosera</i> sp.	sundew
<i>Daucus carota</i>	Queen Anne's lace
<i>Dulichium arundinaceum</i>	three-way sedge
<i>Echinochloa walteri</i>	Walter's millet
<i>Elatine</i> sp.	waterwort
<i>Eleocharis obtusa</i>	blunt spikerush
<i>Eleocharis parvula</i>	least spikerush
<i>Eleocharis quadrangulata</i>	large spikerush

APPENDIX I--Continued.

Scientific name	Common name
<i>Eleocharis</i> spp.	spikerush
<i>Equisetum fluviatile</i>	water horsetail
<i>Erianthus giganteus</i>	sugar-cane plumegrass
<i>Erigeron canadensis</i>	horseweed
<i>Eriocavlon septangulae</i>	mermaidweed
<i>Eupatorium capillifolium</i>	dog fennel
<i>Eupatorium maculatum</i>	joe-pye weed
<i>Eupatorium purpureus</i>	boneset
<i>Eupatorium serotinum</i>	boneset
<i>Euphorbia polygonifolia</i>	seaside spurge
<i>Euthamia graminifolia</i>	goldenrod
<i>Fimbristylis</i> sp.	fimbristylis
<i>Fragaria virginiana</i>	wild strawberry
<i>Fraxinus pennsylvanica</i>	green ash
<i>Fuirena pumila</i>	umbrella grass
<i>Fuirena squarrosa</i>	umbrella grass
<i>Galium</i> sp.	bedstraw
<i>Gaultheria procumbens</i>	wintergreen
<i>Gaylussacia dumosa</i>	dwarf huckleberry
<i>Gerardia maritima</i>	seaside gerardia
<i>Gerardia purpurea</i>	gerardia
<i>Glyceria obtusa</i>	manna grass
<i>Gratiola neglecta</i>	hedge hyssop
<i>Helenium autumnale</i>	sneezeweed
<i>Heleochloa schoenoides</i>	swamp timothy
<i>Hibiscus laevis</i>	smooth rose-mallow
<i>Hibiscus moscheutos</i>	rose-mallow
<i>Hydrocotyle umbellata</i>	pennywort
<i>Hymphoides cordatum</i>	floating heart
<i>Hypericum ellipticum</i>	marsh St. John's wort
<i>Hypericum mutilum</i>	dwarf St. John's wort
<i>Ilex glabra</i>	inkberry
<i>Ilex opaca</i>	American holly
<i>Impatiens capensis</i>	jewelweed
<i>Ipomoea</i> sp.	morning glory
<i>Iris versicolor</i>	blue flag
<i>Iva ciliata</i>	marsh elder
<i>Iva frutescens</i>	high tide bush
<i>Juncus balticus</i>	Baltic rush

APPENDIX I--Continued.

Scientific name	Common name
<i>Juncus effusus</i>	soft-stem bulrush
<i>Juncus roemerianus</i>	black needlerush
<i>Juniperus virginiana</i>	red cedar
<i>Kalmia angustifolia</i>	sheep laurel
<i>Kosteletzkya virginica</i>	saltmarsh mallow
<i>Kuhnia eupatorioides</i>	false boneset
<i>Lactuca serriola</i>	prickly lettuce
<i>Lathyrus japonicus</i>	beach pea
<i>Leersia oryzoides</i>	rice cutgrass
<i>Lemna minor</i>	duckweed
<i>Leptochloa fascicularis</i>	sprangletop
<i>Leptochloa filiformis</i>	sprangletop
<i>Lilium canadense</i>	Canada lilly
<i>Lindernia</i> sp.	pimpernel
<i>Lippia</i> spp.	frog-fruit
<i>Liquidambar styraciflua</i>	sweetgum
<i>Lobelia cardinalis</i>	cardinal flower
<i>Lolium</i> sp.	ryegrass
<i>Ludwigia palustris</i>	water purslane
<i>Lycopodium</i> spp.	club moss
<i>Lycopus virginicus</i>	water horehound
<i>Lysimachia terrestris</i>	yellow loosestrife
<i>Lythrum hyssopifolia</i>	hyssop loosestrife
<i>Lythrum salicaria</i>	purple loosestrife
<i>Maianthemum canadense</i>	Canada mayflower
<i>Malvella leprosa</i>	alkali mallow
<i>Melilotus alba</i>	white sweet clover
<i>Mentha arvensis</i>	wild mint
<i>Mikania</i> sp.	hempweed
<i>Mimulus ringens</i>	monkey flower
<i>Mollugo verticillata</i>	carpetweed
<i>Muhlenbergia asperifolia</i>	alkali muhly
<i>Myrica cerifera</i>	wax myrtle
<i>Myrica gale</i>	sweet gale
<i>Myrica pensylvanica</i>	bayberry
<i>Myriophyllum asiatica</i>	Asian milfoil
<i>Myriophyllum exalbescens</i>	water milfoil
<i>Nelumbo lutea</i>	American lotus
<i>Nuphar Luteum</i>	yellow cow-lily

APPENDIX I--Continued.

Scientific name	Common name
<i>Nymphaea odorata</i>	water lily
<i>Odontites serotina</i>	eyebright
<i>Onoclea sensibilis</i>	sensitive fern
<i>Osmunda regalis</i>	royal fern
<i>Oxalis stricta</i>	yellow wood sorrel
<i>Panicum amarum</i>	beach grass
<i>Panicum</i> spp.	panic grass
<i>Panicum virgatum</i>	switchgrass
<i>Paspalum laeve</i>	smooth paspalum
<i>Peltandra virginica</i>	arrow arum
<i>Phalaris arundinacea</i>	reed canary gras
<i>Phragmites communis</i>	common reed
<i>Pluchea camphorata</i>	camphor weed
<i>Pluchea purpurascens</i>	salt marsh fleabane
<i>Pogonia ophioglossoides</i>	rose pogonia
<i>Polygonum arifolium</i>	tear thumb
<i>Polygonum coccinium</i>	water smartweed
<i>Polygonum hydropiperoides</i>	water pepper
<i>Polygonum monspeliensis</i>	beard grass
<i>Polygonum pennsylvanicum</i>	pinkweed
<i>Pontederia cordata</i>	pickerelweed
<i>Populus deltoides</i>	cottonwood
<i>Potamogeton epihydrus</i>	ribbon pondweed
<i>Potamogeton natans</i>	floating pondweed
<i>Potamogeton pectinatus</i>	sago pondweed
<i>Potamogeton zosteriformis</i>	flatstem pondweed
<i>Prunella vulgaris</i>	self-heal
<i>Puccinellia nuttalliana</i>	Nuttal's alkali grass
<i>Quercus falcata</i>	southern red oak
<i>Quercus laurifolia</i>	laurel oak
<i>Quercus nigra</i>	water oak
<i>Quercus virginianus</i>	live oak
<i>Ranunculus</i> spp.	buttercup
<i>Rhus copulina</i>	winged sumac
<i>Rhus glabra</i>	smooth sumac
<i>Rotala ramosior</i>	rotala
<i>Rubus hispidus</i>	swamp dewberry
<i>Rumex</i> sp.	dock
<i>Ruppia maritima</i>	widgeon grass

APPENDIX I--Continued.

Scientific name	Common name
<i>Sabatia stellaris</i>	marsh pink
<i>Sagittaria latifolia</i>	arrowhead
<i>Sagittaria</i> spp.	duck potato
<i>Salicornia</i> spp.	pickelweed
<i>Salix carolinensis</i>	Carolina willow
<i>Salix nigra</i>	black willow
<i>Saururus cernuus</i>	lizard's tail
<i>Scirpus americanus</i>	three-square bulrush
<i>Scirpus atrovirens</i>	green bulrush
<i>Scirpus acutus</i>	hardstem bulrush
<i>Scirpus cyperinus</i>	woolgrass
<i>Scirpus olneyi</i>	Olney's three-square
<i>Scirpus robustus</i>	alkali bulrush
<i>Scirpus validus</i>	softstem bulrush
<i>Scutellaria lateriflora</i>	mad-dog skullcap
<i>Senecio vulgaris</i>	groundsel
<i>Sesbania marocarpa</i>	sesbania
<i>Sesuvium maritimum</i>	sea purslane
<i>Setaria</i> spp.	foxtail
<i>Sium suave</i>	water parsnip
<i>Solanum carolinense</i>	horse nettle
<i>Solidago</i> spp.	goldenrod
<i>Sonchus</i> sp.	sowthistle
<i>Sparganium</i> spp.	burreed
<i>Spartina alterniflora</i>	cordgrass
<i>Spartina cynosuroides</i>	big cordgrass
<i>Spartina patens</i>	salt meadow grass
<i>Spirea latifolia</i>	American meadowsweet
<i>Spirea tomentosa</i>	hardhack
<i>Stellaria</i> spp.	chickweed
<i>Tamarix pentandra</i>	salt cedar
<i>Thelypteris thelypteroides</i>	marsh fern
<i>Toxicodendron radicans</i>	poison ivy
<i>Triglochin</i> sp.	arrowgrass
<i>Typha angustifolia</i>	narrow-leaf cattail
<i>Typha latifolia</i>	broad-leaf cattail
<i>Utricularia cornuta</i>	horned bladderwort
<i>Utricularia vulgaris</i>	common bladderwort
<i>Vaccinium corymbosum</i>	blueberry

APPENDIX I--Continued.

Scientific name	Common name
<i>Vaccinium macrocarpon</i>	large blueberry
<i>Vallisneria americana</i>	wild celery
<i>Verbascum blattaria</i>	moth mullein
<i>Verbena hastata</i>	blue vervain
<i>Veronica scutellata</i>	marsh speedwell
<i>Viola cucullata</i>	blue-marsh violet
<i>Vitis rotundifolia</i>	muscadine grape
<i>Xanthium spp.</i>	cocklebur
<i>Zizania aquatica</i>	northern wild rice
<i>Zizania miliacea</i>	southern wild rice

APPENDIX II

*Field Collection Data Sheet***EASTERN COTTONMOUTH RADIOTELEMETRY/MARK-RECAPTURE DATA SHEET**

(Chad L. Cross, Dept. Biological Sciences, Old Dominion University, Norfolk, VA, 23529. 757-683-3595)

DATE: OBSERVERS:

BBNWR: Natural Anthropogenic		
SNAKE ID:	radio	PIT tag scale clip
TIME:	FLAG NUMBER:	TREE TAG NO:

SNAKE LOCATION:	upland	shoreline	water	hibernaculum
COVER OBJECT:				DISTANCE to WATER: m
SUN EXPOSURE:	full sun	shade	full shade	
ACTIVITY:	coiled	extended	moving (direction:)	
BEHAVIOR:	passive	aggressive	very aggressive	
ACTION:	flee	approach	stand ground	

PIT READINGS:

TEMPERATURE:	Air:	C	Surface:	C	Soil:	C
CLOUD COVER:	none		partly cloudy		overcast	
PRECIPITATION:	none		light rain		heavy rain	

HABITAT DESCRIPTION: DOMINANT PLANT SPECIES:

DBH and DISTANCES	Tree (>7cm):	cm	Distance:	m	Species:
	Tree (<7cm):	cm	Distance:	m	Species:
COVER (%):	Canopy:		Leaf Litter:		
	Debris:		Vegetation:		
STEMS:	Density:	/sq-m	Height:	m	Species:

NOTES:

VITA

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Banner-Tailed Kangaroo Rats

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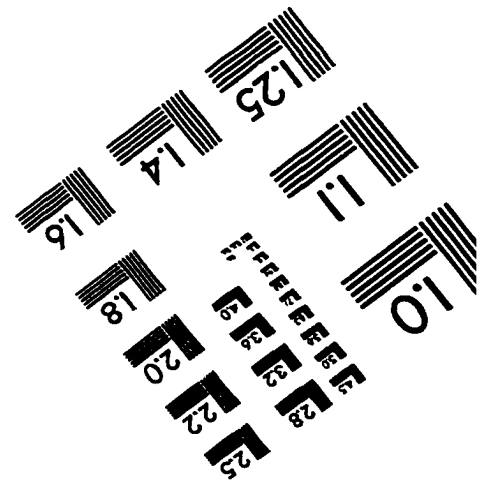
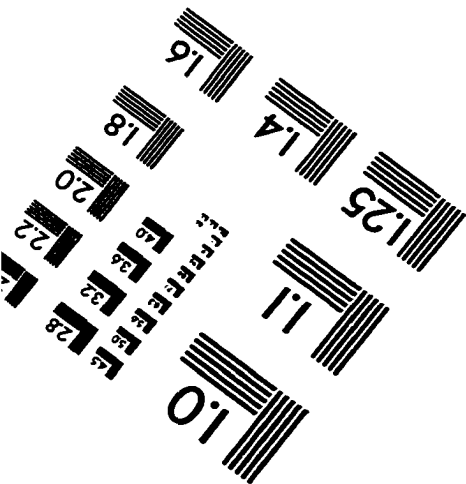
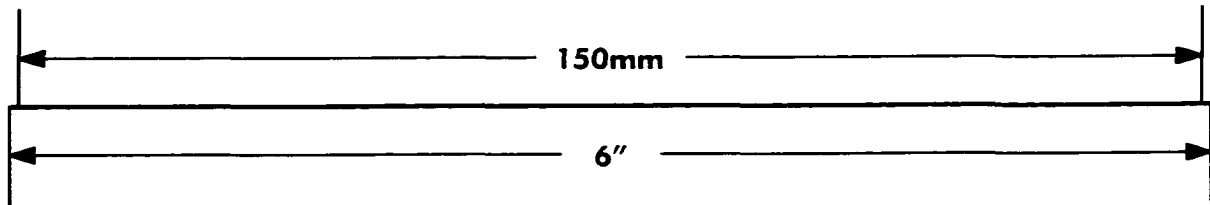
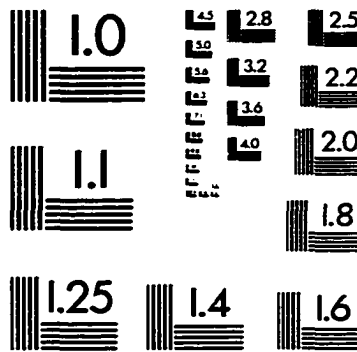
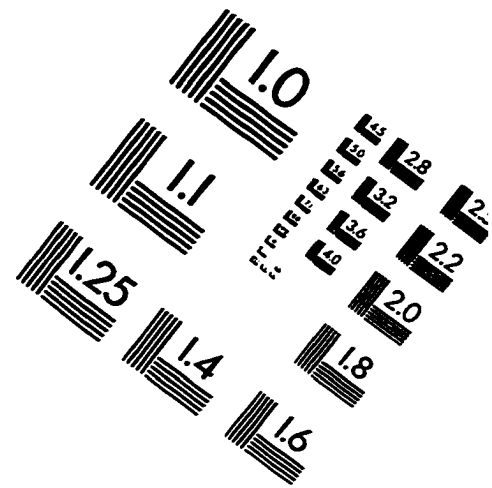
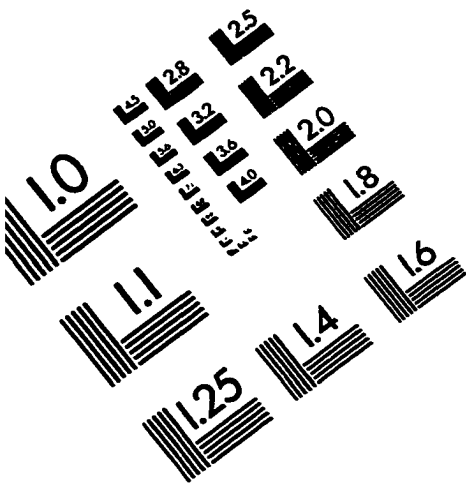
Project: The Analysis of Snake Microhabitat Using Radiotelemetry and Polytomous
Logistic Regression

Doctor of Philosophy

Advisor: Dr. Alan H. Savitzky, Department of Biological Sciences, Old Dominion
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Project: Ecology of the Eastern Cottonmouth (*Agkistrodon p. piscivorus*) at Back
Bay National Wildlife Refuge: A Comparative Study of Natural and
Anthropogenic Marsh Habitats

IMAGE EVALUATION TEST TARGET (QA-3)



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