

Population Abundance and Habitat Requirements of the Marsh Wren
(*Cistothorus palustris*) at Dyke Marsh Wildlife Preserve:
An Urban Conservation Challenge

A thesis submitted in partial fulfillment of the requirements for the degree of
Master of Sciences at George Mason University

By

Sandy C. Spencer
Bachelor of Arts
College of William and Mary, 1984

Lee Talbot, Professor
Committee Chair
Department of Biology

Fall Semester, 2000
George Mason University
Fairfax, Virginia

ACKNOWLEDGEMENTS

I gratefully thank the following persons and entities for the invaluable assistance that made completion of this thesis possible: The National Park Service, George Washington Memorial Parkway, for access to records and the research site; the Washington Biologists' Field Club, Inc. and Friends of Dyke Marsh for funding assistance; Drs. Lee Talbot (advisor), R.Christian Jones, Larry Rockwood, Walter Piper, and Donald T. Gantz, George Mason University; research assistants Alex Chidakel, Vicky McLaughlin, Gigi Kruse, Jennifer Wang, and Hector Castro, for many long hours in difficult field conditions; Dr. Roger Clapp, National Museum of Natural History; John Bazuin, Jr., Virginia Society of Ornithology; Dr. Jared Verner; Frank Smith, U.S. Fish and Wildlife Service, Bombay Hook NWR; Greg Weiler, Joe Witt, and Marcie Heacker, U.S. Fish and Wildlife Service, Mason Neck and Occoquan Bay NWR; Susan Rudy and Jim Rosenstock, National Park Service, National Capital Parks East; Kitty Brant, Air Photographics, Inc.; Gregory P. Justice; Mardi Ruth Thompson; Barry Wood, NPS, for technical assistance with GIS ARCVIEW; James P. Long; and Roger S. Miller. Earlier drafts of this manuscript benefited from many useful comments from Dr. Pete Marra, Smithsonian Environmental Research Center, and Dr. Paul B. Roberston, Texas Parks and Wildlife.

TABLE OF CONTENTS

	Page
Acknowledgements.....	ii
Table of Contents.....	iii
List of Tables.....	iv
List of Figures.....	v
Abstract.....	vi
1. Introduction.....	1
2. Methods.....	7
3. Results.....	17
4. Discussion.....	34
5. Conclusion.....	41
6. Literature Cited.....	42
7. Appendices.....	47

LIST OF TABLES

			Page
1.	Table 1:	Available Habitat vs. Area Used	20
2.	Table 2a:	Male Territory Selection Variables	22
3.	Table 2b:	Proximity to Red-winged Blackbird Areas, Shoreline Profile, and Exposure Variables for Male Territory Selection	22
4.	Table 3a:	Female Territory Selection Variables	25
5.	Table 3b:	Proximity to Red-winged Blackbird Areas, Shoreline Profile, and Exposure Variables for Female Territory Selection	26
6.	Table 4a:	Reproductive Success and Territory Quality	27
7.	Table 4b:	Proximity to Red-winged Blackbirds and Conspicuousness for Reproductive Success	27
8.	Table 5:	Percentages of Breeding Nest Failures by Type	28
9.	Table 6:	Use of Alternative Vegetation for Nest Sites	29
10.	Table 7:	Summary of Surveys of Other Local Marshes	33

LIST OF FIGURES

		Page
1.	Figure 1: Aerial Photos of Dyke Marsh from 1937 to 1996	6
2.	Figure 2: Map of Marshes Surveyed in the Upper Tidal Zone of of the Potomac River:	16
3.	Figure 3: Distribution of Territories, 1998	18
4.	Figure 4: Distribution and Boundaries of Territories, 1999	19
5.	Figure 5: Available Habitat vs. Area Used, 1999	21
6.	Figure 6: Bar Graph of Absolute Density per Territory Class	23
7.	Figure 7: Bar Graph of Proximity to Red-winged Blackbird Areas per Territory Class	23
8.	Figure 8: Bar Graph of Shoreline Profile per Territory Class	24
9	Figure 9: Illustration of Preferred and Avoided Types of Shoreline Profiles	24
10.	Figure 10. Plot of Percent <i>Typha</i> per Breeding Class	26

ABSTRACT

POPULATION ABUNDANCE AND HABITAT REQUIREMENTS OF THE MARSH WREN (*Cistothorus palustris*) AT DYKE MARSH WILDLIFE PRESERVE: AN URBAN CONSERVATION CHALLENGE

Sandy C. Spencer, M.S.

George Mason University, 2000

Thesis Director: Dr. Lee Talbot

In 1998 and 1999, I estimated the abundance of a population of marsh wrens (*Cistothorus palustris*) at Dyke Marsh National Wildlife Preserve based on number of territories. In addition, I estimated the reproductive success based on number of fledglings. For 1999 only, the percent of available habitat used; male and female habitat selection preferences; the variation in territory quality between successful and failed nests; causes of nest failure; and use of alternative vegetation for nest sites were investigated. In 1999, I also surveyed other marshes in the upper tidal zone of the Potomac to verify whether Dyke Marsh contains the only population of marsh wrens in this area. The differences between territories and non-territories for male selection preferences based on seven habitat variables. Nine habitat variables were used to measure differences between breeding and non-breeding territories and between

successful and failed nests. Differences between groups were analyzed using non-parametric tests. Reproductive success was based upon actual number of fledglings.

Thirty-one territories were located in 1998, and 34 in 1999. The population estimate was 38 (31 territorial males and 7 breeding females) in 1998, and 48 (34 territorial males and 14 breeding females) in 1999. This number excludes roving bachelors, and second or third mates of polygynous males. The discrepancy in the female number between years may reflect insufficient manpower to discover all breeding nests in 1998. Reproductive success for 1998 was nine young fledged; for 1999, eleven young fledged. Only 30% percent of available habitat was used by marsh wrens in 1999.

Absolute density of tall, emergent vegetation ($P = 0.003$) and proximity to red-winged blackbirds ($P = 0.011$) were the most significant habitat variables driving male selection preferences. Percent *Typha* spp. was a marginally significant factor ($P = 0.089$) for female selection. No significant difference was detected between successful ($n=5$) and failed ($n=11$) nests in 1999 for any of the variables measured. The majority (79%) of nest failure is due to predation by conspecifics, or interspecific birds, snakes, small mammals. Only four territories used non-cattail vegetation for nest attachment but none of the nests attached to alternative species became breeding nests. A survey of similar tidal marshes in the upper Potomac tidal zone revealed that there are no other breeding

populations of marsh wrens in this area.

Because the local population of marsh wrens has very narrow preferences for nesting territories, has experienced substantial habitat loss over the last few decades, are subject to high rates of predation, and do not appear to be very adaptable to alternative forms of vegetation, the population could be at risk over the long term.

INTRODUCTION

The marsh wren (*Cistothorus palustris*) is a common, marsh-dwelling, insectivorous passerine found throughout Canada and the United States (Leonard and Picman 1987a). The species occupies a wide variety of wet habitats, such as paramo, wet meadow, tall grassland, or marsh (Kroodsma and Verner 1997), and a diversity of marshland habitats as well. It uses numerous species of tall aquatic vegetation for breeding habitat (Ridgeway 1889, Welter 1935, Pearson et al. 1942, Bent 1964, Verner 1965, Kale 1965, Gutzwiller and Anderson 1985, Stevenson and Anderson 1994). This diversity notwithstanding, loss of habitat may mean a decline in abundance.

Marsh wrens were once abundant along the Potomac River close to District of Columbia (Coues and Prentiss 1883, Ridgeway and Forbes 1889, Shufeldt 1927, Cooke 1929, Syphax 1996, Halle 1947, Abbot, n.d.b). By the 1960s a substantial reduction in population size had occurred (Abbot 1963, n.d.c, 1987), and by 1982 wrens were rare (Swift 1982, Syphax 1996) and found in limited locations (Abbot 1987). Marshland was also once extensive along the Maryland and Virginia shores close to the District of Columbia (Swift 1982). This habitat type underwent massive loss due to infilling and development, dredging for sand and gravel (Hartwell 1970), and erosion. Dyke

Marsh also experienced a substantial loss of area in the 1960s and 1970s (Figure 1). More recently, ecological degradation via invasive plant species such as porcelain berry (*Amphelopsis brevipedunculata*) and morning glory (*Ipomoea sagittata*) has occurred. Today, it appears to be the only habitat in the upper Potomac tidal zone (from the fall line to Mason Neck) capable of supporting a population of marsh wrens.

A census of the marsh wren population at Dyke Marsh has not been conducted previously. cursory observations in June 1950 yielded eighty-seven singing males and 38 non-singing males in December 1958 (Davis 1950 and 1958). An assessment of the Dyke Marsh population and habitat quality is needed to establish a baseline for a monitoring program and a basis for developing a management plan to maintain the wren population. Marsh wrens are so specific in their habitat requirements that monitoring them may have the further benefit of further benefit of furnishing a valuable tool to detect vegetation changes in the marsh.

This study seeks to: 1) estimate the current abundance of the population at Dyke Marsh and the degree of habitat saturation; 2) determine which habitat characteristics are most important for male territory selection and female settlement preferences; 3) measure reproductive success (based on the number of fledglings) for at least one year and assess the habitat variables related to success; 4) verify whether Dyke Marsh is the only suitable marsh in the upper

Potomac tidal zone capable of supporting a population; and 5) examine this population's use of alternative types of vegetation besides cattail for nest sites.

Habitat Requirements

All marsh wren habitats have two crucial requirements for nest sites: exposure to standing water (although intertidal marshes that periodically lack standing water are acceptable) and tall, dense vegetation for nest support and cover (Kroodsma and Verner 1997, Gutzwiller and Anderson 1985). Several erect and closely-spaced stalks or limbs are needed to provide the strength and height to support a bulky nest at least several centimeters above the water surface (Gutzwiller and Anderson 1987). Dense vegetation also provides more protection against mammalian and avian predators (Leonard and Picman 1987a). Adequate shoreline (interface between vegetation and open water or drainage channels) is also essential, as flooding provides additional predator deterrence (Welter 1935, Burger 1985, Kale 1965, Verner 1965, Picman et al. 1993, personal observations 1998-1999). Water depth has been shown to be negatively correlated with mammalian predation (Burger 1985, Picman et al. 1993). Experiments with fake marsh wren nests containing quail eggs overwhelmingly demonstrated a relationship between types of predation, rates of predation, and water depth (Picman et al. 1993). Nests that are situated adjacent to water's edge are ensured longer flooding duration in a tidal marsh.

Hence wrens prefer shorelines for nest sites. However, too-deep water precludes establishment of tall vegetation, which wrens require for nest support.

So there are limits as to how deep the water may be.

A territory must also be large enough to accommodate at least one courting center, which consists of a cluster of dummy nests (male-constructed nests that do not become breeding nests). These serve to confuse and deter predators (Shufeldt 1927, Leonard and Picman 1987b).

Marsh wrens exhibit a preference for colonial living and this clumping of territories may have social stimulating effects that are more important than micro-habitat features (Kale 1965). Preferential habitat may be forsaken and lower quality habitat adopted in order to maintain proximity to the territories of other marsh wrens (personal observation). Isolated territories are rare (Kale 1965). Colonial life may also lower predation via cooperative predator detection, mobbing behavior, and predator satiation (Picman et al. 1988).

Direct competition between marsh wrens and red-winged blackbirds (*Agelaius phoeniceus*) frequently leads to agonistic interactions and mutual nest predation. However, the intensity of the competition is mitigated somewhat by spatial segregation. This results because marsh wrens prefer higher cattail density (Linz et al. 1996, Picman 1977b, 1984, 1988). Interspecific competition with red-winged blackbirds and conspecific competition influence the spatial configuration of territories. The former causes compression, the latter

expansion. The end result is a dynamic tension between the two forces (Picman 1984 and 1988).

A territory's shoreline profile is a feature that may figure importantly in habitat selection. For example, a levee with a sharp drop off bordering the water channel or a gradual slope with a wide margin of spadderdock are the extremes in gradients of variation. Marsh wrens seem to prefer the former and tend to avoid the latter (personal observation). Also, the amount of shoreline a territory possesses may also be important, as wrens consistently prefer to build nests close to the water's edge (Kale 1965, Verner 1965).

Food in the form of insects is assumed to seldom be a limiting factor (Gutzwiller and Anderson 1987), because the emergence of insects in marshes is frequent (Burger 1985). Only marshes that meet habitat quality requirements and are of sufficient size will sustain a population of marsh wrens. Such sites in the upper tidal zone of the Potomac are extremely limited in number.

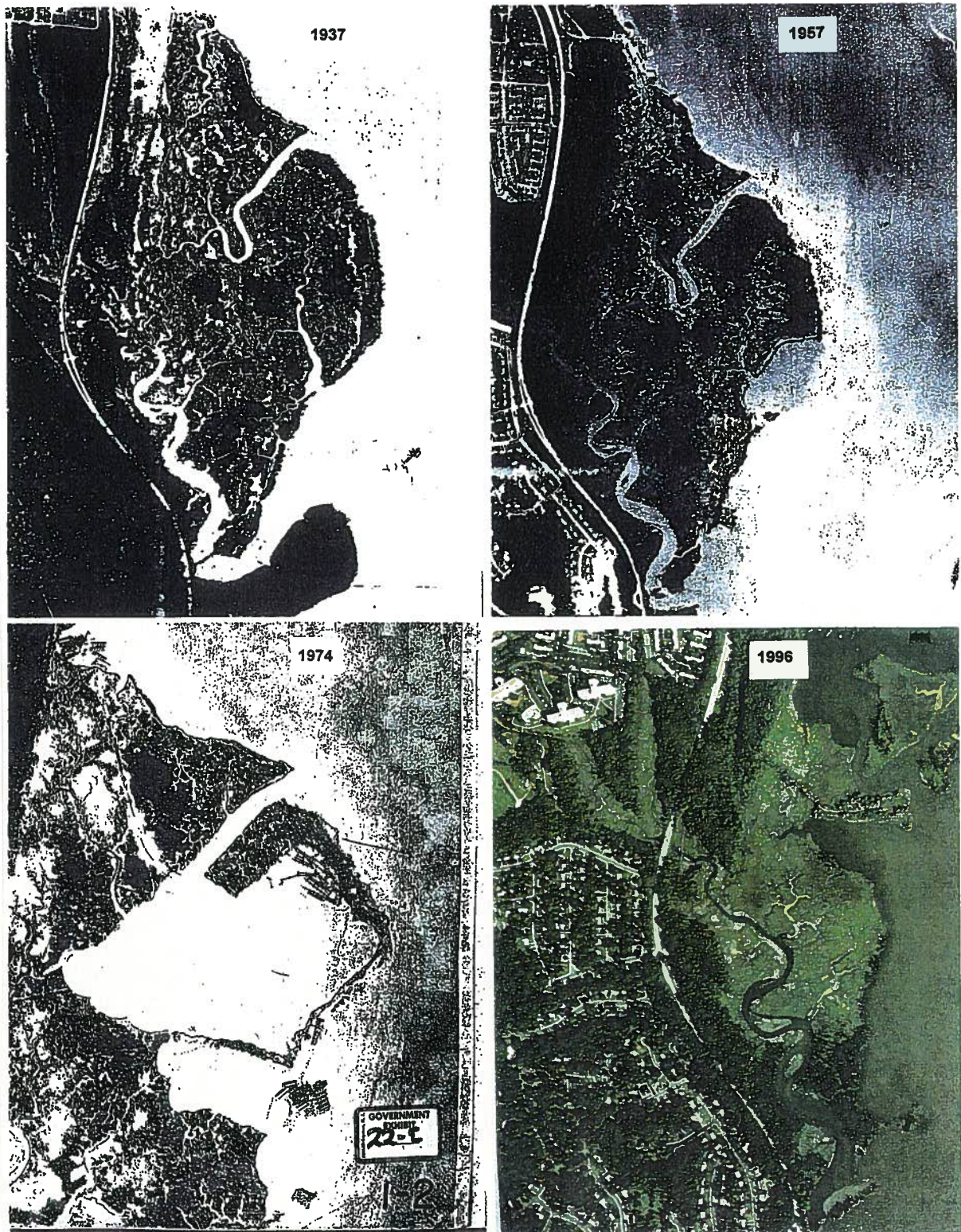


Figure 1: Aerial Photos of Dyke Marsh from 1937 to 1996 Depicting Reduction in Area (photos courtesy of the National Park Service and USGS)

METHODS

Field observations were conducted during the breeding seasons of 1998 and 1999 from the start of the season in early May until the end of the season in late August. Observations were made on a daily basis of habitat use and territory occupation, and of wren nests (appearance and location of new nests and nest fate). Some habitat measurements were made at the end of the season when breeding activity had ceased, including, but not limited to, vegetation density, percent *Typha* spp., and flooding depth. In 1998, only the principle investigator was involved; in 1999, five research assistants were employed in gathering nest and territory data.

Study Site Description

Dyke Marsh Wildlife Preserve is a natural, freshwater, tidal marsh located approximately two miles south of the District of Columbia on the Virginia side of the Potomac River, well within the densely-populated suburbs of the nation's capital. About 5,000 to 7,000 years old, and only a remnant of its former size (Briggs 1954, NPS), its area now is approximately 154 hectares (380 acres).

Population Estimates

Population size was based on the number of territories. The number of males was assumed to equal the number of male-defended territories and the number of females was based on the number of male territories containing an egg nest (henceforth referred to as breeding territories). The estimate assumes a 1:1 sex ratio (Kroodsma and Verner 1997) and excludes roving bachelors.

Although wrens are both monogamous and polygynous, (Kroodsma 1983, Picman and Belles-Isles 1987, Kroodsma and Verner 1997) the extent of polygynous mating was not measured in this study. Therefore, the estimate is likely to be lower than the actual abundance.

Habitat Saturation

In this study, habitat saturation is defined as the amount of available habitat used for breeding territories by marsh wrens. Available habitat is that area of high marsh dominated by *Typha* and *Acorus spp.* that is also well-flooded. In some marsh wren populations territory size fluctuates throughout the breeding season; some investigators have compensated for this variation by multiplying the average size by the number of territories when computing area used (Welter 1935, Kale 1965, Leonard and Picman 1987a). However, the Dyke Marsh population exhibited such a wide range of territory sizes (and monitoring throughout the season did not detect any substantial fluctuation) that

area used was obtained by summing areas of individual territories. The degree of habitat saturation was obtained by comparing the total amount of available habitat to the total area of territories. Available habitat and area of territories (for 1999 only) were calculated using a 1:200 aerial photo (Fairfax County 1998) geo-rectified in UTM's for use with GIS ARCVIEW.

Male-defended territories were located and boundaries determined through the use of call playbacks and by direct observation of male aerial displays or singing from their perches (Picman and Belles-Isles 1987). This method was a modified version of Kale (1965), Verner (1965), and Welter (1935). My method differed since an overview of all territory perimeters was not always possible at Dyke Marsh. In some cases boundaries had to be inferred from naturally occurring landscape features such as vegetation breaks, water's edge (Kroodsma and Verner 1997), or from territorial defense behavior in response to playback recordings (Manci and Rusch 1988). The process was repeated over the course of several days to confirm territory locations. A map of the marsh derived from an aerial photograph (1994; scale 1:200) was used to relate territorial boundaries to the vegetation mosaics and other marsh features. Territory boundaries were monitored throughout the breeding season to detect changes.

Male and Female Habitat Selection Preferences

The objective was to determine if there were significant differences beyond what is expected by chance between male selection and female selection of territories. For male selection, seven habitat variables were measured to characterize and distinguish between territories and non-territories: absolute density of vegetation, percent *Typha spp.*, flooding depth, exposure (number of cardinal directions exposed to wind and fetch), proximity to red-winged blackbird areas, distance from colonial center, and shoreline profile. For female selection, nine habitat variables were measured to distinguish between breeding and non-breeding territories: the previous seven plus shoreline length and territory area (size). Breeding territories are defined as those male territories in which a female established a breeding nest. Because shoreline length and territory area are wren-dependent variables, these could not be measured for non-territories and thus were not included in the design for male selection. This approach resulted in three distinct categories: a) territory (based on the presence of a singing male and territorial behavior); b) breeding territory (based on observation of egg nests); and c) non-territory, sites that were similar to wren territories but were not claimed by a wren (neither nests found nor singing heard). Each category had ten replicates resulting in 30 sample sites which could then be grouped according to the line of questioning desired: for male habitat selection, territory (n=20) versus non-territory (n=10); for female

habitat selection, breeding territory (n=10) versus non-breeding territory (n=10).

Sample sites were selected randomly after breeding season was well underway (late July). The timing also served to reveal regions for the investigator's selection of non-territory sites. For this category, sites close to and far from the colonial center were selected to avoid bias.

Percent *Typha*, absolute density of tall, emergent vegetation, and flooding depth were measured at twenty-foot transects that were established along the shoreline of each sample site and, if in a territory, set to intersect with as many nests as possible. For non-territories, distance from colonial center and proximity to red-wing black bird areas were also measured from the transect, as they possessed no area dimensions as defined by wrens. The two vegetation attributes (absolute density and percent *Typha spp.*) were measured using a hybrid approach which combined features of the standard point-quarter method and the quadrat method (Appendix 1). Flooding depth was measured only once at each site and represents the distance between the exposed marsh floor at low tide and high tide mark on stakes placed at each transect (Appendix 2).

Exposure was based on the number of cardinal directions directly exposed to a long fetch of wind and wave action. The colonial center is defined as that cluster that contained the largest number of territories. A circle was drawn around this cluster, its center point determined, and the distance between the center point and the closest edge of each territory (or the transect for non-

territories) was measured. For proximity to red-winged blackbird areas, each sample was assigned to one of four categories: 1) well segregated; 2) abuts red-winged black bird area; 3) red-winged blackbird area overlaps up to 25%; and 4) 25% or greater overlap. Shoreline profiles were categorically characterized: 1) no apparent shoreline; 2) gradual, borders broad expanse of low marsh; 3) borders narrow channels and rivulets; 4) a combination of 3 and 5; and 5) levee with steep drop off bordering open water or channels. Shoreline length was measured directly using a walk-chain. Territory area was described in the habitat saturation section.

Reproductive Success

Reproductive success in this study was defined as at least one young successfully fledged for a given nest (Kale 1965, Kroodsma and Verner 1997).

An alternative approach to measuring success is the modified Mayfield nest survival method, which is based on the total number of days a nest survives from discovery to destruction or fledging of young (Hensler and Nichols 1981,

Johnson 1979). However, because marsh wrens build many dummy nests per territory, there may be hundreds of nests in a population's breeding area.

Including dummy nests in an analysis of success would risk bias in the direction of severe overestimation if the Mayfield nest survival method was employed.

Therefore, only the egg nests (breeding nests) were considered and the sample

size equals the entire population of breeding nests.

The cause of nest failure was one method used to gauge habitat quality. For example, low vegetation density may result in either higher predation due to higher conspicuousness, or in wind blow-over due to greater exposure and lessened stability. Alternatively, nest destruction by blow-over or flooding may be more an artifice of the builder than habitat quality if the nest was not well-attached or of insufficient height. Only the breeding nests of the 10 randomly-selected breeding territories were analyzed. The nest attributes measured were: number of cattail stems used for nest attachment, absolute density of vegetation, the height of the nest from the marsh floor, conspicuousness (number of cardinal directions from which the nest was not surrounded by vegetation and therefore conspicuous), distance from colonial center; proximity to red-winged blackbird areas, territory size, flooding depth under the nest, and the number of dummy nests in the territory at the time the nest was active. Female diligence in nest defense was not measured due to shortage of manpower for making sustained observations.

The success or failure of each breeding nest was also recorded. Causes of failure were grouped into three categories: Type I, predation by conspecifics or interspecific bird species, snakes, and small mammals such as mice; Type II, predation by large mammals such as raccoons; or Type III, destruction due to storms and high winds. It is useful to distinguish between the two types of biotic

predation as it provides insight into habitat quality and selection by wrens.

Larger mammals are less frequent in deeper areas of the marsh. Because predation by conspecifics, interspecific bird species, snakes or mice is difficult to distinguish with certainty when the contents are absent, these sources were grouped together as Type I. Evidence for Type I predation is an intact, undamaged nest that is either emptied of its contents before completion of term or containing damaged contents, such as pecked eggs. Type II predation is evidenced by a severely torn nest with its lower half usually pulled down (Appendix 3).

Use of Other Vegetation Types

For every nest in the breeding and non-breeding categories, the species of vegetation used to support the nest was noted. This enabled the frequency of use of alternative species (other than *Typha spp.*) to be determined.

Comparison with Similar Local marshes

Other marshes comprised of tall, emergent vegetation in the upper tidal zone of the Potomac River were surveyed during the breeding season to determine the extent to they support a population of marsh wrens. After a preliminary survey of numerous potential habitats in the upper tidal zone, the following sites were chosen for closer examination on the basis of having a large

area of cattail marsh: Kenilworth Marsh Restoration Area on the Anacostia River in Washington, D.C.; Great Marsh, of the Mason Neck National Wildlife Refuge; Mattawoman Creek; and Marumsco Creek of the Occoquan Bay National Wildlife Refuge (Figure 2). The presence and general abundance of wrens, dominant vegetation type, and degree of flooding were noted. Surveys were conducted at the height of the breeding season (June or July) during the morning hours in fair, calm weather to maximize the likelihood of hearing singing males. Bombay Hook, a large saltwater marsh on the Delaware Bay, was also surveyed for comparison with a site with a large population of marsh wrens.

Statistical Analysis

For habitat selection preferences, all thirty sites were first analyzed for significant variation between territories ($n=20$) and non-territories ($n=10$) (male selection preferences), and then between breeding ($n=10$) and non-breeding territories ($n=10$) (female selection preferences) using the Mann-Whitney U-test for all variables measured in discrete, incremental units or using the Chi Square Test of Independence for variables measured in artificially assigned categorical values. The same analytical procedures were applied to the success category variables to determine significant differences between successful nests ($n = 5$) and failed nests ($n = 11$). All other investigations are descriptive and qualitative in nature and were not statistically analyzed.

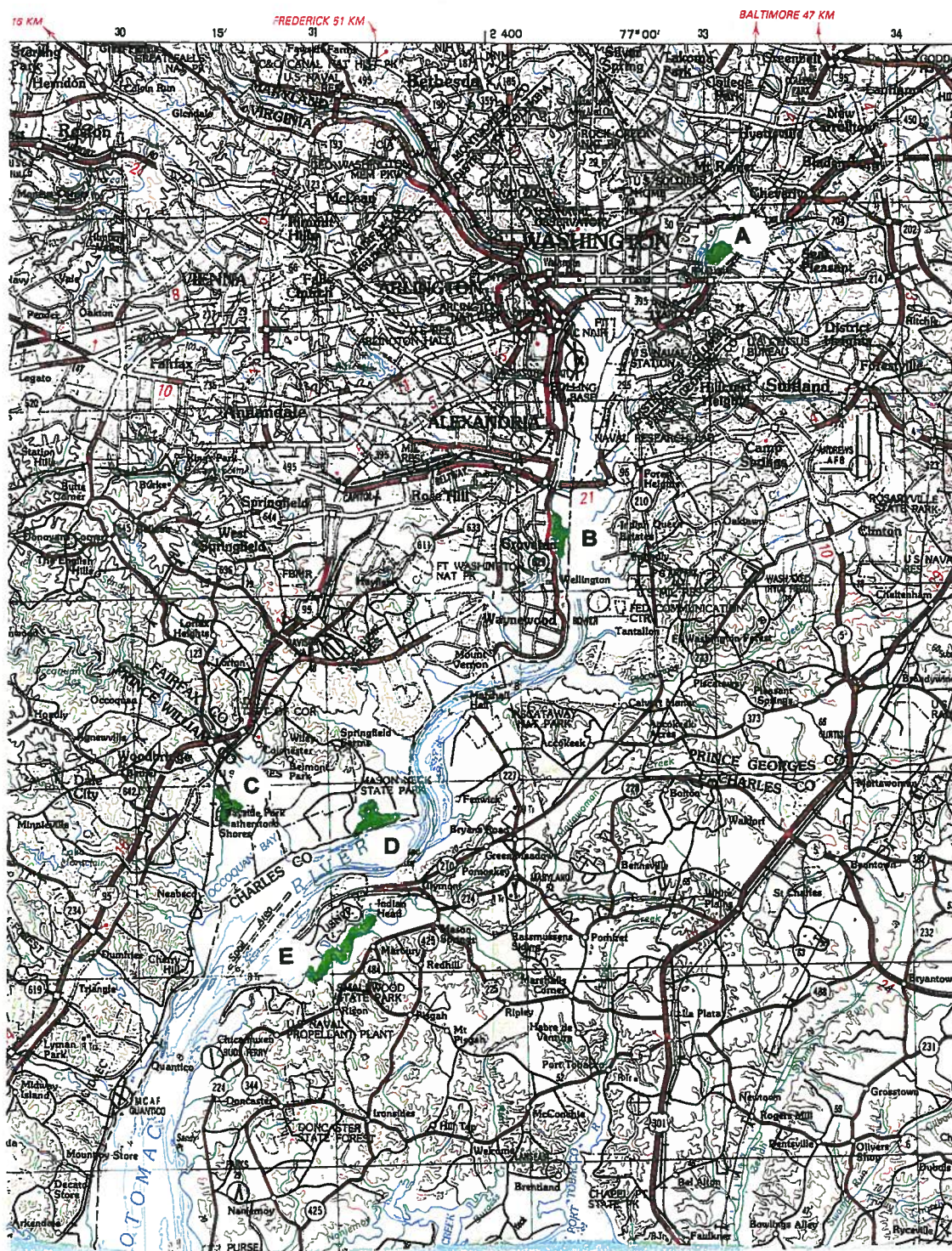


Figure 2: Marshes Surveyed in the Upper Tidal Zone of the Potomac River. A) Kenilworth Marsh; B) Dyke Marsh; C) Marumsco Creek; D) Great Marsh; E) Mattawoman River. (USGS Hydrological Survey, 1989).

RESULTS

Population Estimates

Thirty-one male-defended territories and seven breeding territories were located in 1998. Thus, the minimum population was 31 males and 7 females ($N = 38$). In 1999, there were 34 male-defended territories and 14 breeding territories. Thus the minimum population was 34 males and 14 females ($N = 48$) for that year. These numbers are certainly underestimated since roving bachelors and the second and third females of polygynous males were not counted. The low number of breeding territories in 1998 compared to 1999 probably reflects inadequate manpower to locate all of the breeding nests rather than a true discrepancy.

Habitat Saturation

In 1999, wrens claimed four new territories in the south section not claimed in 1998. In the north section, two marginal territories from the previous year were dropped (Is1T8 and Is2T1), and two territories were overtaken by the neighboring male wren (Is1T4 and East Is1T2). Figures 3 and 4 illustrate the distribution territories for 1998 and 1999 respectively.



Figure 3: Distribution of Marsh Wren Territories, 1998.

Marsh Wren Territories and Available Habitat, 1999

Colored polygons = territories
Outlined polygons = available habitat



Figure 4: Distribution of Marsh Wren Territories, 1999.

For 1999, the total available habitat was 19.08 hectares (47.16 acres); the total area of all 34 was 5.6 hectares (13.89 acres) or about 30% (Table 1, Figure 5). Territory areas and available habitat were not measured in 1998.

Table 1 : Available Habitat vs. Area Used, 1999.

Available Habitat	190,852.00 m ² (19.08 hectares)
Area Used	56,215.89 m ² (5.62 hectares)
Percent of Available Habitat Used	30%

Male and Female Habitat Selection Preferences

Male Selection Preferences: Absolute density of tall, emergent vegetation, proximity to red-winged blackbird areas, and shoreline profile differed significantly between territories and non-territories (Mann-Whitney U test/Pearson Chi Square, $P < 0.05$) (Tables 2a and 2b, Figures 6-8). Territories tended toward higher absolute density of tall, emergent vegetation than non-territories. More territories were well-segregated (the lower categories, 1 and 2) from red-winged blackbird areas than were non-territories. Most wrens avoided selecting territories with no shorelines (category 1) or with shorelines that were broad, gradual slopes (category 2) covered with spatterdock (*Nuphar luteum*) and preferred the higher categories of shoreline profiles, particularly the levee with steep drop-off type of shoreline (Figure 9).

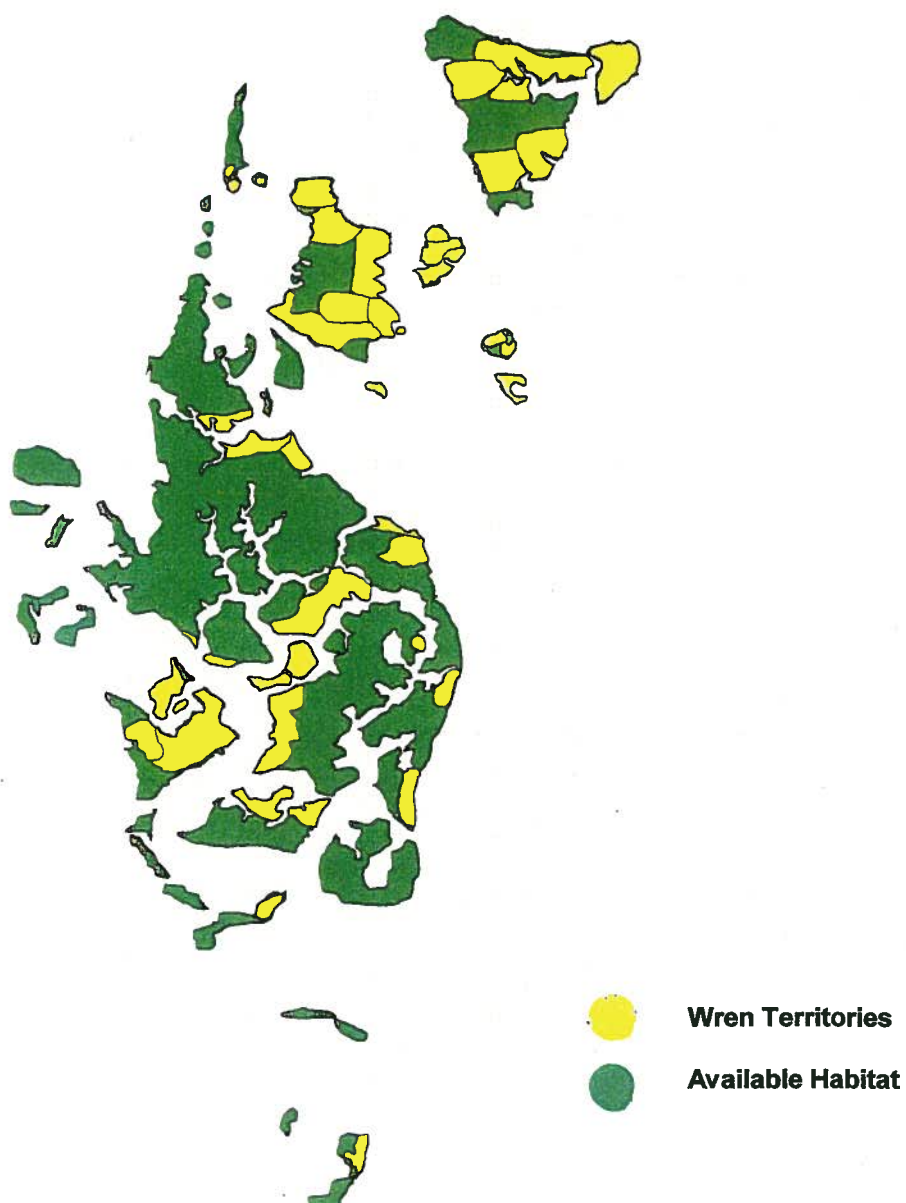


Figure 5: Available Habitat versus Area Used

Table 2a : Male Territory Selection Variables (Territory class: n=20, non-territory class, n=10; Testing at Alpha = 0.05 level; Mann-Whitney U Test), ranked from highest to lowest significance.

Variable	Means, Standard Deviation		Significance
	Territories	Non-Territories	
Absolute Density (stems per m ²)	67.8 6.0	42.9 4.4	0.003
Flooding depth under nests, cm	37.9 1.2	35.7 1.9	0.328
Percent <i>Typha spp.</i>	0.62 0.06	0.71 0.09	0.328
Distance from Colonial Center, m	314.7 48.3	402.3 68.4	0.350

Table 2b: Proximity to Redwinged Blackbirds, Shoreline Profile, and Exposure Variables for Male Territory Selection (Territory class: n=20, non-territory class, n=10; Testing at Alpha = 0.05 level; Pearson Chi Square Test for Independence).

Proximity to RWBB			Shoreline Profile			Exposure		
Category	NT	Terr	Category	NT	Terr	Category	NT	Terr
1	2 20%	8 40%	1	0	2 10%	1	3 30%	6 20%
2	0	7 35%	2	7 70%	4 20%	2	3 30%	6 16.7 %
3,4*	8 80%	5 25%	3,4*	3 30%	7 35%	3	3 30%	12 40%
			5	0	7 35%	4	1 10%	7 23.3 %
Pearson Chi Sq.		8.95	Pearson Chi Sq.		9.09	Pearson Chi Sq.		3.86
Significance		0.011	Significance		0.028	Significance		0.276

* Categories 3 and 4 were collapsed because they are similar and to increase the power of the chi-square test.

Key: Exposure: 1-4 = number of cardinal directions; Shoreline Profile: 1 = no apparent shoreline; 2 = gradual slope; 3 = borders narrow channels and rivulets; 4 = combination of 3 & 5; 5 = steep drop off. Proximity to Red-winged Blackbirds: 1 = well-segregated; 2 = abuts territory; 3 = 25% overlap; 4 = >25% overlap.

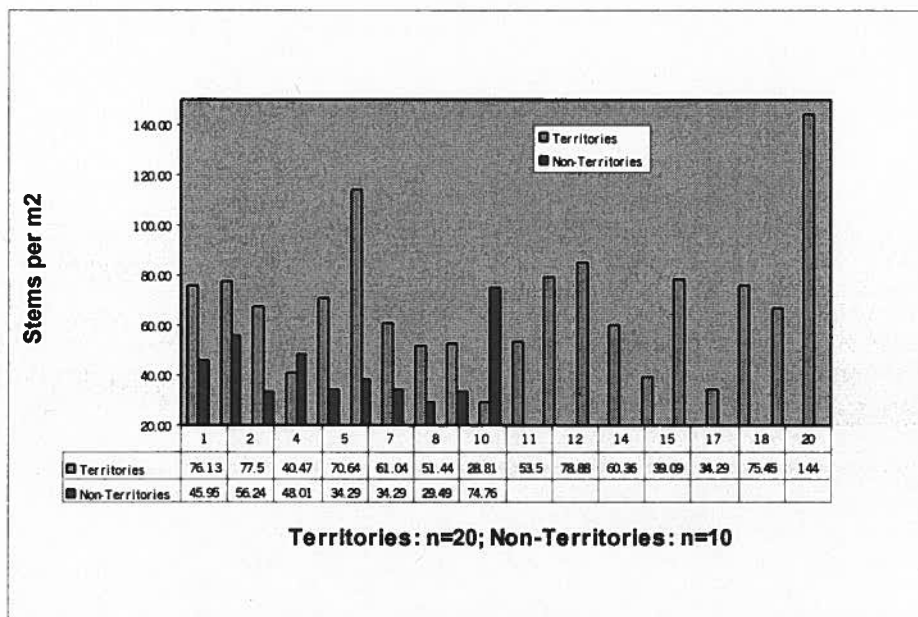


Figure 6: Absolute Density of Tall, Emergent Vegetation per Territory Class

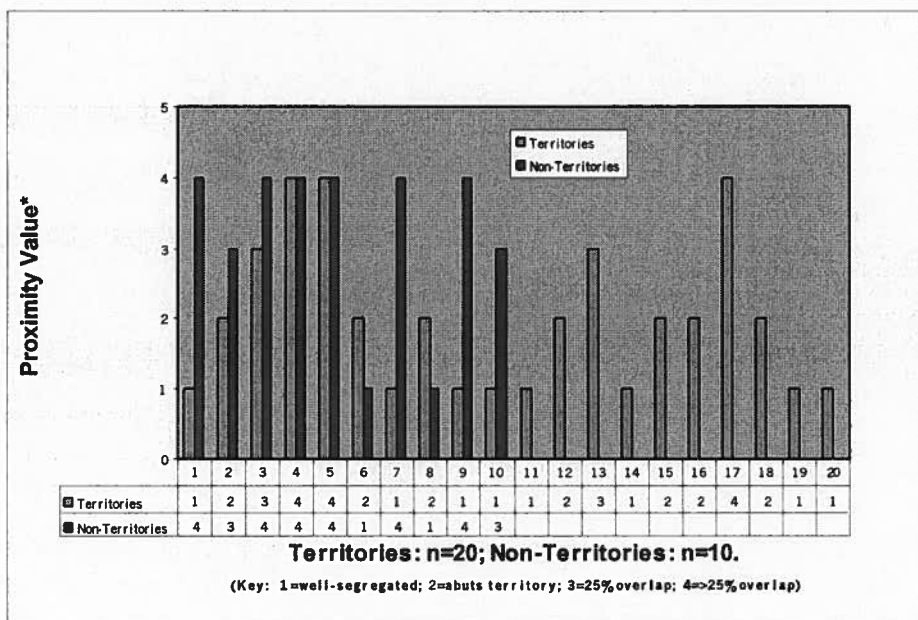


Figure 7: Proximity to Red-winged Blackbird Areas per Territory Class

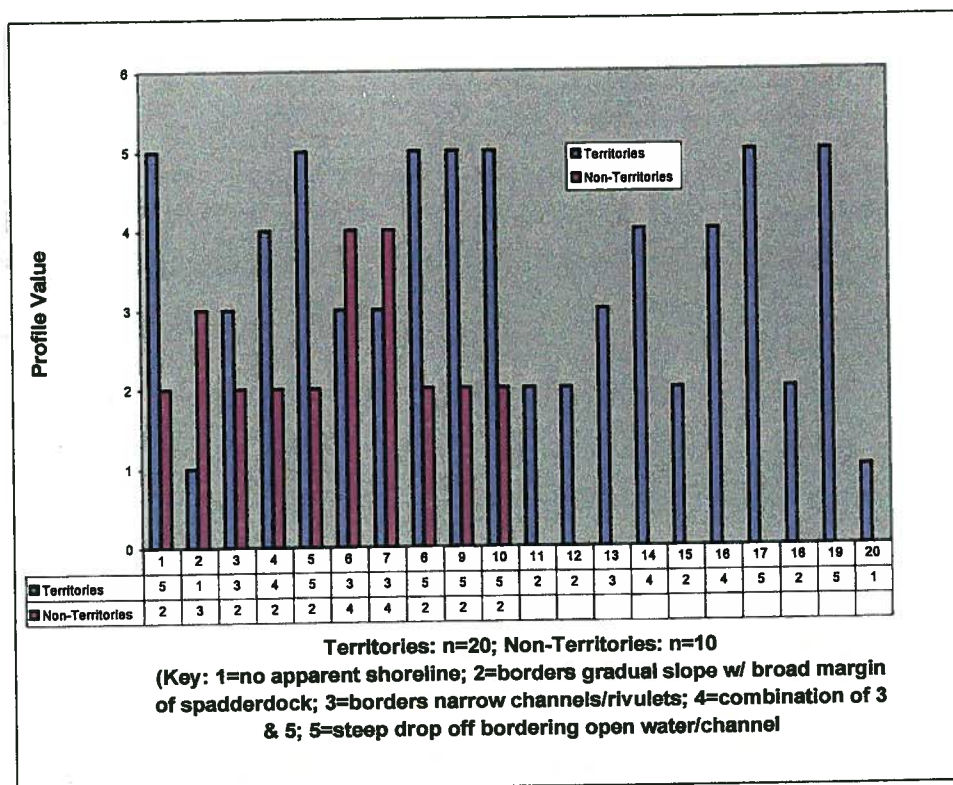


Figure 8: Shoreline Profiles per Territory Class

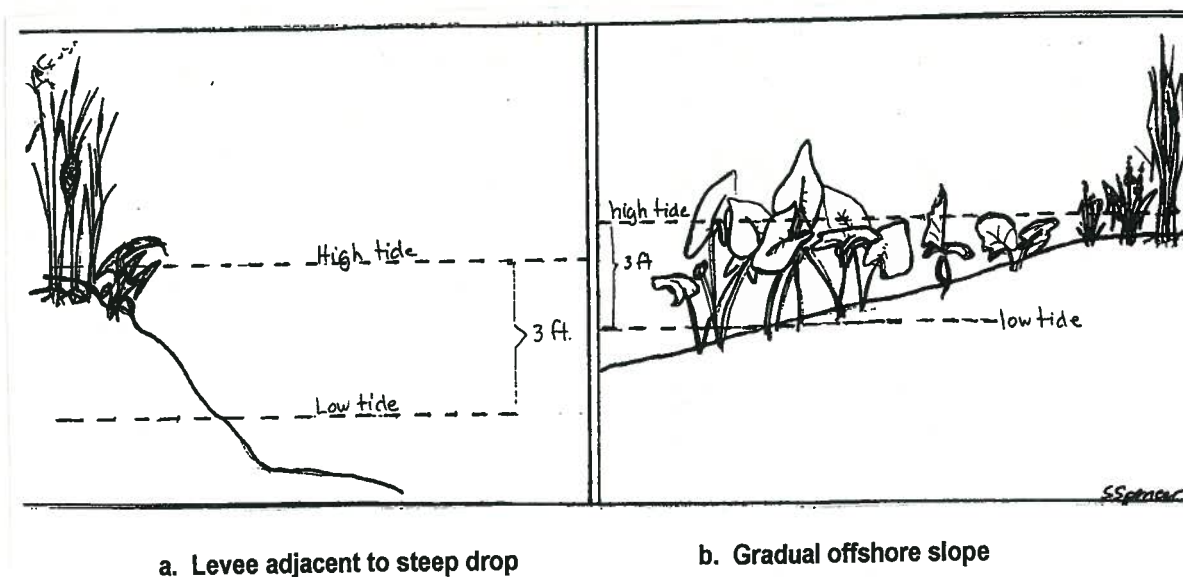


Figure 9: Preferred and Avoided Types of Shoreline Profiles

Female Selection Preferences: there was no significant difference between breeding and non-breeding territories for any of the variables measured.

However, percent *Typha spp.* was marginally significant (Mann-Whitney U test, $P = .089 < .10$) (Table 3a and 3b, Figure 10).

Reproductive Success and Nest Failure

Reproductive success for 1998 was 9 fledglings from 7 breeding nests and a total of 31 eggs or 29% (9/31). Reproductive success for 1999 was 11 fledglings from 20 breeding nests and a total of 80 eggs or 14% (11/80). No significant difference between successful and failed nests could be detected (Tables 4a and 4b). The variable area was close to being marginally significant and discussed later.

Table 3a : Female Territory Selection Variables (breeding territories $n = 10$; non-breeding territories, $n = 10$; Testing at Alpha = 0.05 level; Mann-Whitney U Test), ranked from highest to lowest significance.

Variable	Means, Standard Deviation		Significance
	Breeding	Non-Breeding	
Percent <i>Typha spp.</i>	0.72 0.05	0.52 0.08	0.089
Distance from Colonial Center, m	240.8 63.3	388.6 68.2	0.165
Area, m ²	2262.8 662.5	1341.0 347.5	0.218
Absolute Density (stems per m ²)	64.0 7.4	71.5 9.7	0.529
Shoreline length, m	106.9 32.0	101.0 14.8	0.684
Flooding depth under nests, cm	38.3 1.8	37.5 1.7	0.912

Table 3b: Proximity to Redwinged Blackbirds, Shoreline Profile, and Exposure Variables for Female Territory Selection (Breeding Class: n=10, non-breeding class, n=10; Testing at Alpha = 0.05 level; Pearson Chi Square Test for Independence), ranked from highest to lowest significance.

Exposure			Shoreline Profile			Proximity to RWBB		
Category	NB	Br	Category	NB	Br	Category	NB	Br
1	2 20%	1 10%	1	1 10%	1 10%	1	4 40%	4 40%
2	0	2 20%	2	4 40%	0	2	4 40%	3 30%
3	3 30%	6 60%	3,4*	3 30%	4 40%	3	1 10%	1 10%
4	5 50%	1 10%	5	2 20%	5 50%	4	1 10%	2 20%
Pearson Chi Sq.		6.00	Pearson Chi Sq.		5.43	Pearson Chi Sq.		0.476
Significance		0.112	Significance		0.143	Significance		0.924

*Categories 3 and 4 collapsed because they are so similar and to increase the power of the chi-square test.

Key: Exposure: 1-4 = number of cardinal directions; Shoreline Profile: 1 = no apparent shoreline; 2 = gradual slope; 3 = borders narrow channels and rivulets; 4 = combination of 3 & 5; 5 = steep drop off. Proximity to Red-winged Blackbirds: 1 = well-segregated; 2 = abuts territory; 3 = 25% overlap; 4 = >25% overlap.

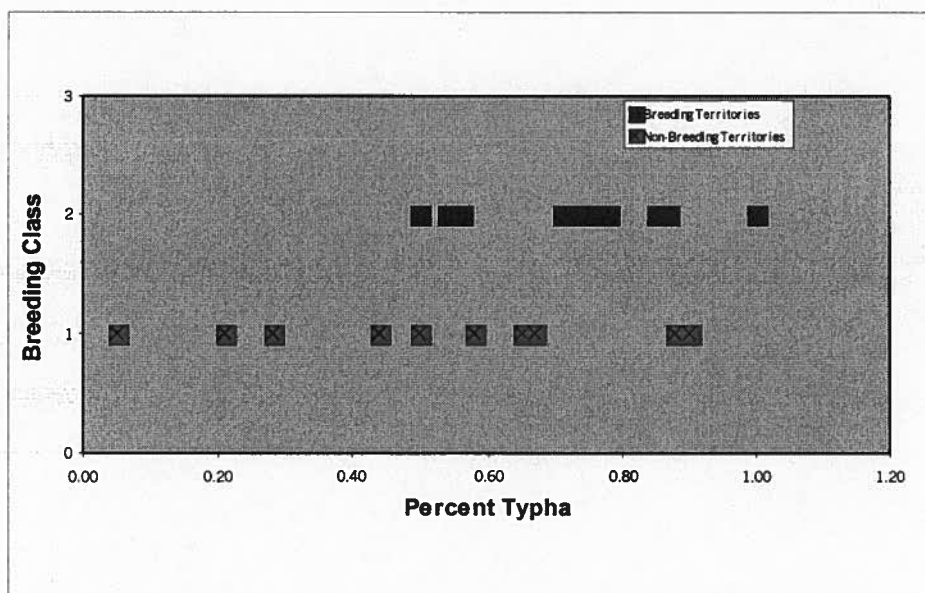


Figure 10: Plot of Percent *Typha* per Breeding Class

Table 4a: Success category variables (Successful nests: n=5, failed nests, n=11; Testing at Alpha = 0.05 level; Mann-Whitney U Test), ranked from highest to lowest significance.

Variable	Means and Standard Error		Significance
	Successful Nests	Failed Nests	
Area	4154.2 1094.7	2515.2 650.5	0.118
Flooding depth under nests, cm	40.7 1.5	38.6 1.8	0.562
Number of Cattail Stems	3.5 0.3	3.2 0.3	0.562
Absolute Density (stems per m ²)	65.6 11.0	60.4 7.7	0.713
Distance from Colonial Center, m	261.7 86.3	239.3 70.7	0.714
Height	133.8 4.4	129.5 8.6	0.875
Number of Dummy Nests	9.5 3.7	6.6 1.1	0.958

Table 4b: Proximity to Red-winged Blackbirds and Conspicuousness Variables for Success Class (Successful nests: n=5; failed nests: n=11; Testing at Alpha = 0.05 level; Pearson Chi Square Test for Independence).

Proximity to RWBB			Conspicuousness		
Category	Failed	Successful	Category	Failed	Successful
1	3 50%	3 50%	1,2	4 57.1%	3 42.9%
2	4 100%	0	2	6 75%	2 25%
3,4*	4 66.7%	2 33.3%	3	1 100%	0
Pearson Chi Sq.		2.81	Pearson Chi Sq.		1.039
Significance		0.245	Significance		0.595

*Categories were collapsed because they are similar and to increase the power of the chi-square test.

Key: Exposure: 1-4 = number of cardinal directions; Shoreline Profile: 1 = no apparent shoreline; 2 = gradual slope; 3 = borders narrow channels and rivulets; 4 = combination of 3 & 5; 5 = steep drop off. Proximity to Red-winged Blackbirds: 1 = well-segregated; 2 = abuts territory; 3 = 25% overlap; 4 = >25% overlap.

The majority (93%, 13/14) of unsuccessful nests were lost to some type of predation in 1999, of which 76% was lost to Type I predation (Table 5). Only one breeding nest was lost to storm damage. This nest was exposed to a long fetch of open water to the north.

Table 5 : Percentages of breeding nest failures by type

Type of Failure	Number	Percentage
Type I: Predation by conspecifics, interspecifics (other birds, snakes, or mice)	11	79%
Type II: Predation by large mammal (i.e. racoon)	2	14%
Type III: High winds, storms	1	7%

Use of Alternative Vegetation by Marsh Wrens at Dyke Marsh

The favored tall emergent vegetation type for this population was primarily cattail (*Typha* spp.) and secondarily sweetflag (*Acorus* spp.). Only four territories (12% of all 34 territories) were found to have nests attached to tall emergent species other than *Typha* spp. (except where an occasional sweetflag or rush stem was incorporated along with cattail stems). In one territory, marshmallow, *Hibiscus moscheuto*, was consistently used, as well as *Typha*, although not simultaneously. In another, several nests were attached to common reed, *Phragmites australis*, while a majority of the other nests were attached to *Typha*. Although in all cases the nests were well built, strongly

attached, well flooded underneath, and usually inconspicuous, both males remained bachelors. Two other male territories contained some nests attached to alternative vegetation (tidewater marshhemp, *Amaranthus cannabinus* and rush, *Juncus spp.*) but did become breeding territories. However, the breeding nests of both territories were attached to the traditional *Typha spp.*, not to alternative vegetation (Table 6).

Table 6: Use of alternative vegetation for nest sites

Territory ID	Plant species used:	Breeding Territory?
NNT3	<i>Hibiscus moscheuto</i>	No
HRT2	<i>Juncus spp.</i>	Yes
NST1	<i>Amaranthus cannabinus</i>	Yes
BGT2	<i>Phragmites australis.</i>	No

Note: In the two breeding territories (HRT2 and NST1), the breeding nests were not attached to the alternative species, but to *Typha spp.*

Comparison with Similar Local Marsh Sites

Great Marsh, part of the Mason Neck National Wildlife Refuge on the Virginia side of the Potomac River, was surveyed on July 28, 1999. This marsh is very similar in appearance to Dyke Marsh: with broad expanses of tall emergent vegetation intersected by channels of open water or choked with spatterdock. However, dense cattail does not occur in large patches as at Dyke Marsh; it instead occurs in narrow strips or mixed with other species. The dominant tall emergent plants are sweetflag (*Acorus calamus*), sedges (*Cyperus*

and *Scirpus* spp.), and wild rice (*Zizania aquatica*). Buttonbush (*Cephalanthus occidentalis*) and marshmallow (*Hibiscus moscheutos*) were also interspersed throughout, and, in some areas, rafts of morning glory (*Ipomea sagittata*) were beginning to bring down the cattails and sweetflag as it does at Dyke Marsh.

Marsh wrens were neither seen nor heard during the three-hour period.

However, five nests were discovered. Four nests were found clumped close to each other in one part of the marsh, and a single nest was found in another section. Of the four nests that were grouped together, two were in good condition, and two appeared to be start-ups that were never completed. One of the good nests was attached to about three stems of sedge, and one stem of arrow arum. The other good nest was attached to one stem of cattail. Both were in vegetation that was leaning over. The two start-up nests were in a sweetflag/cattail mix that had been flattened. All of the nests appeared to be a few weeks old, made of cattail leaves, and the two good nests included fluff.

The isolated fifth nest was made mostly of grass, some cattail, attached to dead cattail and at a lower height from the marsh floor. It was also very exposed to the Potomac River.

All five nests were located near the open water and subjected to regular flooding underneath. The number and locations of nests found suggest the presence of one or two wrens.

Marumsco Creek is part of the Occoquan Bay National Wildlife Refuge

and was surveyed in July 1999. Its upper reaches contain a freshwater tidal marsh consisting primarily of cattail and sweetflag and low marsh species (arrow arum, spatterdock, and pickerelweed). The marsh floor is much softer than at Dyke Marsh, suggesting slightly lower elevation. In all but one patch, the cattail is less dense than at Dyke Marsh. Marsh wren presence was detected in this dense patch of cattail by discovering 4 or 5 marsh wren nests, all rather loosely constructed and estimated to be from one to two weeks old. The builder was neither seen nor heard. The number and spacing of nests suggests the presence of only one wren.

Mattawoman River. Both shores of the river were surveyed on July 19, 1998. Several cattail marshes line its southern shore near the mouth of the river, but the cattail is not dense. The survey was conducted by powerboat, which precluded going ashore to look for nests. No wrens were heard or seen at any time during the survey.

Kenilworth Marsh Restoration Area, Anacostia River. The return of this species to Kenilworth in 1996 was viewed as one of the best success indicators of the wetland's reconstruction (Syphax 1996). Wrens were heard singing in June and July 1999 (one to 5 wrens), however, no nests were found (Greg Goff 2000, personal communication). The reconstructed area is subject to three-foot diurnal tides and cattail is the dominant species, but it is less dense than at

Dyke Marsh.

Bombay Hook National Wildlife Refuge, Delaware Bay, DE: This site was chosen for comparison because wrens thrive in great abundance here. Although it is a saltwater tidal marsh featuring different vegetation species from Dyke Marsh, it is useful for comparison of vegetation structure.

Dyke Marsh and Bombay Hook differ greatly in size: roughly 380 acres (153.79 hectares) and 21 square miles (54.39 square kilometers), respectively. Due to the immense size of Bombay Hook, it was not possible to obtain abundance data on marsh wrens from a one-day visit and the annual point count surveys yield only relative abundance and frequency, not absolute numbers, for marsh wrens. Nevertheless, along a 1.5 mile (2.4 km) stretch of a small creek feeding the Leipsic River singing wrens were frequently encountered and could always be heard within earshot both up and downstream.

Dyke Marsh and Bombay Hook also differ as to wetland type; Dyke Marsh is a tidal freshwater marsh, Bombay Hook is a tidal saltmarsh. Despite differences in dominant vegetation, a striking similarity between their respective wren populations is evident: both prefer to build their nests in stable, taller vegetation which affords some height above tidal flooding. At Bombay Hook, nests were found in groundsel tree (*Bacchus spp.*), *Spartina alterniflora*, and in *Phragmites spp.* adjacent to a levee or source of flooding. All nests examined were between 103.74 to 148.2 cm high, constructed mostly of *Spartina spp.*

leaves, tight and durable. Although broadleaf cattail, *Typha latifolia*, was present at the freshwater impoundments at Bombay Hook, marsh wrens were not observed in these stands nor using *T. latifolia* for nest construction.

Another noticeable difference was that redwing blackbirds were not sympatric with marsh wrens in the small area surveyed at Bombay Hook. There is some spatial segregation between the two species also at Dyke Marsh, due largely to preferred density of vegetation, but the patterns of vegetation zonation at Bombay Hook are even more starkly contrasted and may explain, partially at least, the greater degree of segregation at Bombay Hook. In summary, the two sites were similar in having tall, durable emergent vegetation structure and regular flooding. Table 7 summarizes the findings of the local surveys.

Table 7: Summary of surveys of other local marshes

Site	Wrens heard	Nests present	Poss. # wrens	Flooding	Cattail density*
Kennilworth	yes	no	1-2	adequate	less dense
Great Marsh	no	yes	1-2	adequate	less dense
Marumsco	no	yes	1	adequate	less dense
Mattawoman River	no	unknown	unknown	adequate	less dense

*Overall, compared to Dyke Marsh

DISCUSSION

Population Estimate and Habitat Saturation

Two seasons of observations yielded similar number of territories (31 and 34) located in the same general regions except for four completely new territories in the south section and two abandoned territories in the north section in 1999.

None of new south territories were selected by female wrens. These facts suggest that the marsh was at maximum saturation for both years, and that suitable nest locations are apparently limited by narrow wren habitat preferences and possibly social constraints which eliminates selection of most (70%) of available marshland. That more than eighty singing males were counted at the height of the breeding season in 1950 before substantial loss of marsh habitat due to sand and gravel dredging in the late 1950s and the 1960s, but only 31 and 34 were counted in 1998 and 1999 respectively, supports the premise that substantial reduction in the number of hectares of quality nesting habitat reduces the abundance of wrens in a population.

For male territory selection, the density of tall, emergent vegetation and proximity to red-winged blackbird areas appear to be most significant habitat variables that drive selection and that distinguish territories from non-territories.

This is in accord with intuitive predictions in that early in the season before the cattail has had an opportunity to reach full height, wrens may select on the basis of density of pre-existing cattail (mostly in the form of dead stems), site philopatry, and red-winged black bird activity. The mutually agonistic relationship between wrens and red-winged blackbirds is keen early in the season before density of tall, emergent vegetation is sufficient to effect spatial segregation. The role of red-winged blackbirds in wren territory selection may not be independent from the stem density factor. Because marsh wrens prefer less rigid and more dense vegetation than do red-winged blackbirds, the two factors are negatively correlated. The denser and more supple the vegetation, the fewer the redwinged blackbirds (Ozesmi 1999). Red-wing blackbirds also avoid marsh wrens, their most important nest predator (Picman 1988).

Shoreline profile was a weakly significant factor in determining territory. Most territories (70%) possessed shoreline profiles that were either steep drop offs, bordering channels and rivulets, or some combination of the two. Only 30% of territories possessed no shoreline at all or bordered broad margins of low marsh (vegetated with spatterdock, *Nuphar luteum*). There may some relationship between shoreline profile and duration of flooding for a tidal marsh. The upper edges of gradually sloping shoreline profiles are usually the last to flood and the first to become exposed on outgoing tides. They therefore

experience shorter periods of flooding duration than do the levees with steep drop-off profiles that are closer to the source of flooding.

Similarities between territories and non-territories with respect to the other variables may be partly due to artifice of the research design, since non-territories were chosen by the investigator based on flooding, density of *Typha*, and proximity to water's edge.

The importance of distance to the colonial center as a factor in male territory selection may have been partially obscured by a possible establishment of a second colonial center in the southern sections of the marsh which would include NST1, EST2, BGT1, BGT3, BGT4, BGT5, BGT6, BGT7, BGT8 and BGT9 (Fig. 4).

For female settlement preferences, percent *Typha* was the only attribute that differed, and only marginally, between breeding and non-breeding territories. Breeding territories had slightly higher percentages of *Typha* in the vegetation transects (situated among the nests) than did non-breeding territories, suggesting that while this may be important, some other attribute(s) may be driving preferential selection among females. Perhaps males had already selected all the best territories based on the same attributes sought by females. Picman (1977a, 1997c) suggests that females may base territory selection on the frequency of aggressive interactions with other females. Male quality was not examined in this study. However, it was not found to be a factor in female choice in a previous study on female settlement preferences (Leonard and

Picman 1987b). Further research on female territory selection at Dyke Marsh is necessary.

Reproductive Success and Nest failure

In general, territory quality did not vary significantly between successful and failed nests with respect to any of the variables measured. However, a cautionary note on interpreting the results is in order here due to the sample size, which was too small to accommodate normal variation. That the area was close to marginally significant ($P=.118$) in this study contradicts the findings in a previous study in two Manitoban marshes, in which there was no direct relationship between territory size and reproductive success (Leonard and Picman 1988). There may be an indirect relationship through polygyny, which is a function of area (Picman 1977a). Picman (1977a) found that in polygynous populations, increases in polygyny and particularly the density of females, may contribute to high rates of conspecific nest mortality by the male and second female when the first female was absent. Thus, a smaller territory occupied by a single, monogamous pair could potentially have greater reproductive success than a larger territory containing multiple, competitive females. This argument suggests a negative correlation between success and territory size and is contradictory to the results of the Dyke Marsh study. A possible explanation for the contradiction is that one exceptionally large successful territory at Dyke

Marsh may have produced an outlier effect which skewed the mean for this class.

Although Leonard and Picman (1987b) showed that more nests are successful and fledge more young in denser vegetation and deeper water, most nests at Dyke Marsh failed due to Type I predation (the most difficult type to avoid), even in high quality territories. Marsh dwelling passerines tend to suffer the highest nest mortality rates, mainly through predation by hawks, crows, owls, snakes and small mammals, but also from other marsh-dwelling species such as red-wing black birds and conspecifics (Ricklefs 1969, Burger 1985, Picman 1988). Although predation rates from mammals decrease with increase of water depth (Picman et al. 1993), it provides little protection against avian predators, particularly conspecifics. Other studies have shown that the greatest predator on marsh wren nests in the deepest and densest parts of the marsh are conspecifics (Picman 1977a, Picman 1984, Picman and Belles-Isles 1987, Picman et al. 1993). This behavior may be a spacing mechanism (Picman and Belles-Isles 1987, Picman 1988). More research is needed to determine the relative importance of conspecific nest destruction and interspecific predation within the Dyke Marsh population.

Use of Alternative Vegetation

In an early local record (Oberholser 1918), several marsh wrens were

discovered singing in a patch of *Solidago altissima*, giant goldenrod, in an unimproved part of Potomac Park (on the Potomac River, adjacent to Washington, D.C.). Even though there were no ponds or cattails, marsh wrens had been returning to this site for many years after destruction of much the cattail marsh by dredging operations. This is the only record of local marsh wrens adapting to a different habitat. Although it is useful to know the extent to which the Dyke Marsh population employs alternative vegetation for nest sites, the data from one year are inconclusive for making predictions about future adaptability. Had usage of alternative vegetation been much greater than 12%, it might have been indicative of greater adaptability or that the population is further along on a gradient of change. The fact that none of the breeding nests attached to alternative forms of vegetation (although these were very durable and available early in the season) does indicate that females will not accept alternative forms for nest sites.

Comparison to Similar Local marshes

At Dyke Marsh, territories are either not established at all or are soon abandoned where the density of cattail is not above 50%. This may explain why wrens have not yet reestablished a breeding population in the Kenilworth marsh and at other local marshes on a permanent basis as they lacked large enough cattail stands of sufficient density. The reason why much of these marshy areas

is not used as breeding territories is a function of wetland creation dynamics. A wetland's geomorphological and hydrological regimes dictate its vegetation composition, dominance, and flooding. The vigorous tides and accompanying strong currents create a typical elevation gradient from tidal streams out into adjoining marshes. A common feature is a slightly elevated levee along the margin of the channel, where overflowing water deposits much of its sediment load. The slightly elevated ground created by tidal depositions creates a favorable condition for cattail to out-compete obligate wet species and to become very dense. The age of a marsh is a factor also. Low marshes are usually geologically younger than high marshes. All factors being equal, high marshes (more favorable for cattail stands) require a longer time to form (Mitsch and Gosselink 1993). The other marshes surveyed in this study may either be slightly younger than Dyke Marsh, or are experiencing subsidence of the marsh floor, or increased flooding, resulting in lower cattail density. Even much of the south section of Dyke Marsh has not yet progressed from early successional low marsh to a more stable, mature, high marsh with the abundance of dense cattail communities as found in the north section. This fact notwithstanding, the net result is that currently Dyke Marsh is the only site remaining in the upper tidal zone of the Potomac with sufficient suitable habitat for a breeding population.

CONCLUSION

The rate at which the Dyke Marsh marsh wren population declined over the last few decades (since massive habitat loss due to dredging) may have been substantial, but there is little concrete information. In absence of these data, close monitoring of the population is all the more imperative for assessing the stability of the current population. Compression onto limited quantities of suitable nesting habitat has resulted in only thirty percent of available habitat being used by wrens at Dyke Marsh. Available habitat comprises only twelve percent of the entire preserve, therefore, actual use by marsh wrens for nesting territories is only 3.6%. Predation is a major factor affecting this population. While this may have always been the case, larger populations with larger habitats can better absorb losses due to predation. Protection of the remaining habitat from reduction or degradation due to expansion of invasive plants, erosion, and restoration of lost habitat is strongly recommended to ensure persistence of this population over the long term.

LITERATURE CITED

- Abbott, J. 1963. Washington National Airport Bird Hazard Survey, Fourth Quarterly Report, August to October 13. Smithsonian Archives, Box 4, Accession Number 93-027.
- Abbott, J. 1987. Locations for unusual, unique, or rare wildlife in Fairfax County, Virginia. Unpublished. Smithsonian Archives, Box 8, Accession Number 93-027.
- Abbott, J. (N.D.)a Alexandria waterfront: a naturalist's paradise. Unpublished. Smithsonian Archives, Box 4, Accession Number 93-027.
- Abbott, J. (N.D.)b Bird checklists for D.C. Area, New Alexandria, Roaches Run, Belle haven Marina, and Dyke Marsh from 1948 to 1962. Unpublished. Smithsonian Archives, Box 3, Accession Number 93-027.
- Abbott, J. (N.D.)c Wildlife recorded at Dyke Marsh and vicinity, East Fairfax County, Virginia, 1946-1976. Unpublished. Smithsonian Archives, Box 4, Accession Number 93-027.
- Barbour, M.G., burke, J.H., and Pitts, W.D. 1987. Terrestrial Plant Ecology, 2nd. Ed. The Benjamin/Cummings Publishing Company, Inc. Menlo Park, CA.
- Bent, A.C. 1964. Life Histories of North American Nuthatches, Wrens, Thrashers, and Their Allies. Dover Publications, Inc. New York. pp.235-236.
- Briggs, S.A. 1954. Washington--City in the Woods. Audubon Society of the District of Columbia, Inc.
- Burger, J. 1985. Habitat Selection in Temperate Marsh-Nesting Birds. *In* Habitat Selection in Birds (Martin L. Cody, ed.) Academic Press, Inc., Orlando.
- Clapp, R. 1997, July. Smithsonian Institution, Museum of Natural History, Division of Birds. Personal communication.
- Cooke, M.T. 1929. Proceedings of the Biological Society of Washington: Birds of

the Washington, D.C., Region. 42: 1-80.

Coues E., & Prentiss, D.W. 1883. Avifauna Columbiana: Being a list of birds ascertained to inhabit the District of Columbia (Second Edition). Government Printing Office. Washington, D.C.

Davis, E.G. 1950. Birds of the Season: April-July 1950. *Atlantic Naturalist*. 6(1): 24-25.

Davis, E.G. 1958. Birds of the Season: November 1957 through January 1958. *Atlantic Naturalist*. 13(2): 120-122.

Goff, G. 2000. USGS Patuxent Wildlife Research Center, personal communication, November 10.

Gutzwiller, K.J. and Anderson, S.H. 1987. *Habitat suitability index models: marsh wren*. U.S. Fish and Wildlife Service. Biological Report 82(10.139). June.

Halle, L.J. 1947. Spring in Washington. Johns Hopkins University Press. Baltimore and London.

Hartwell, E. 1970. Dyke Marsh today. *Atlantic Naturalist* 25(1): 3-7.

Hensler, G.L. and Nichols. X. 1981. The Mayfield method of estimating nesting success: A model, estimators and simulation results. *Wilson Bulletin* 93 (1); 42-53.

Johnson, D.H. 1979. Estimating Nest Success: The Mayfield method and an alternative. *The Auk* 96 (4): 651-661.

Kale II, H.W. 1965. Ecology and bioenergetics of the Long-billed Marsh Wren (*Telmatodytes palustris griseus*) in Georgia salt marshes. Nuttall Ornithological Club, No. 5. Cambridge, Massachusetts.

Kroodsma, D.E. 1983. Marsh wrenditions. *Natural History* 9: 43-46.

Kroodsma, D.E. and Verner, J. 1997. The Marsh Wren (*Cistothorus palustris*). In The birds of North America, No. 308. (A. Poole and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia, and the American Ornithologists' Union, Washington, D.C.

Leonard, M.L. and Picman, J. 1988. Mate choice by marsh wrens: the influence of male and territory quality. *Animal Behavior* 36: 517-528.

Leonard, M.L. and Picman, J. 1987a. Nesting mortality and habitat selection by marsh wrens. *The Auk* 104: 491-495.

Leonard, M.L. and Picman, J. 1987b. The adaptive significance of multiple nest building by male marsh wrens. *Animal Behavior* 35: 271-277.

Linz, G.M., Blixt, D.C., Bergman, D.L., and Bleier, W.J. 1996. Responses of red-winged blackbirds, yellow-headed blackbirds, and marsh wren to glyphosate-induced alterations in cattail density. *Journal of Field Ornithology* 67(1): 167-176.

Manci, K.M. and Rusch, D.H. 1988. Indices to inconspicuous waterbirds. *Journal of Field Ornithology* 59(1): 67-75.

Metz, K.J. 1991. The enigma of multiple nest building by male marsh wrens. *The Auk* 108(1): 170-173.

Mitsch, W.J. and Gosselink, J.G. 1993. Wetlands, 2nd Ed. Von Nostrand Reinhold, New York. p. 271.

Oberholser, H.C. 1918. The season. IX. June 15 to August 15, 1918. Washington Region. *Bird Lore*. 20(5): 360.

Ozesmi, S.L. and Ozesmi U. 1999. An artificial neural network approach to spatial habitat modelling with interspecific interaction. *Ecological Modelling* 116: 15-31.

Pearson, T.G., Brimley, C.S., and Brimley H.H. 1942. Birds of North Carolina. North Carolina Department of Agriculture. Bynum Printing Co. Raleigh, NC. p. 260.

Peterjohn, B.C., Sauer, J.R., and Link, W.A. 1996. The 1997 and 1995 summary of the North American breeding bird survey. *Bird Populations* 3: 48-66.

Picman, J. 1977a. Intraspecific nest destruction in the long-billed marsh wren (*Telmatodytes palustris palustris*). *Canadian Journal of Zoology* 55: 1997-2000.

- Picman, J. 1977b. Destruction of eggs by the long-billed marsh wren (*Telmatodytes palustris palustris*). *Canadian Journal of Zoology* 55: 1914-1920.
- Picman, J. 1984. Experimental study on the role of intra- and inter-specific competition in the evolution of nest-destroying behavior in marsh wrens. *Canadian Journal of Zoology* 62: 2353-2356.
- Picman, J. and Belles-Isles, J.C. 1987. Intraspecific egg destruction in marsh wrens: a study of mechanisms preventing filial ovicide. *Animal Behavior* 34: 236-246.
- Picman, J. 1988. Behavioral interactions between North American marsh-nesting blackbirds and marsh wrens and their influence on reproductive strategies of these passerines. *Protocol of the International Ornithological Congress* 19: 2624-2634.
- Picman, J. Leonard, M. And Horn, A. 1988. Antipredation role of clumped nesting by marsh-nesting red-winged blackbirds. *Behavioral Ecology and Sociobiology* 22: 9-15.
- Picman, J., Milks, M.L., and Leptich, M. 1993. Patterns of predation on passerine nests in marshes: effects of water depth and distance from edge. *The Auk* 110(1): 89-94.
- Ridgeway, R., & Forbes, S.A. 1889. The Ornithology of Illinois, Part I: Descriptive Catalogue, Vol. I. State Laboratory of Natural History. H.W. Rokker, Springfield, IL. p.99.
- Shufeldt, R.W. 1927. The life history of the Long-Billed Marsh Wren: A curiosity in American ornithological biography. *The Oologist* 44(1):2-4.
- Stevenson, H.M. and Anderson, B.H. 1994. The Birdlife of Florida. University Press of Florida. Gainesville, FL. p. 486.
- Stewart, R.E. and Robbins, C.S. 1958. Birds of Maryland and the District of Columbia. North American Fauna, Number 62. U.S. Fish and Wildlife Service. Government Printing Office. Washington, D.C.
- Swift, B. 1982. Birds of the District of Columbia.
- Syphax, S. 1996. Long-billed Marsh Wren sings again in the nation's capital. *Park Science: Integrating Research and Resource Management*. National Park Service-U.S. Department of the Interior 16(4), 9.

Smithsonian Institution. National Museum of Natural History. Division of Birds.
Cistothorus palustris eggs from Virginia in USNM. USNM Catalogue
Numbers B23432-438, B23440-441, B23446-456, B24782-786, B35942-950,
B40461-464, B40953-957, B46387. Record retrieval date June 16, 1996.

Verner, J. 1965. The breeding biology of the long-billed marsh wren. *The Condor* 67: 6-30.

Verner, J. 1971. Survival and dispersal of male long-billed marsh wrens. *Bird Banding* 42 (2); 92-98.

Welter, W.A. 1935. The natural history of the long-billed marsh wren. *The Wilson Bulletin* 47 (1); 3-34.

APPENDIX 1: VEGETATION SAMPLING AND DENSITY METHODS

Vegetation Sampling

The standard point quarter or plotless method does not lend itself well to the dense and overlapping character of vegetation growth at Dyke Marsh, nor does it adequately capture the vegetation characterization of nest sites, thus the hybrid version was devised. Transects of 20 feet (6.096 meters) in length with five randomly-selected points on each were set. Rather than measure the point to plant distance, a one-foot (.3048 meter) radius around each point was used in which the absolute density of each species of tall emergent vegetation was counted. This method then more closely resembles the transect belt (Lindsey 1955 in Barbour et al. 1987). As nests often occur along a shoreline or rivulet, the transect lines were set in such a way as to intersect with a breeding nest (in breeding territories) or as many dummy nests as possible in non-breeding territories. For non-territories, transects were laid in the densest cattail along the shore. Where the shoreline was too sinuous for a single straight line, the transect made turns, but kept to 20 feet.

Density

1. Calculation of area of transects in m²: Each 20' transect had five 1' radius circles.

Circle Area	= $\pi (r^2)$
	= $3.14 (.3048)^2$
	= .2917 m ²
.2917m ²	= area of 1 circle
.2917 x 5	= area of all circles in one transect = 1.458m ²

2. Calculation of vegetation density: divide # stems per transect by 1.458m²
Example: $111/1.458 = 76.13$ stems/m²

APPENDIX 2: FLOODING DEPTH METHOD

High marsh flooding durations are up to four hours or less on each tidal cycle (Mitsch *et al.* 1993) and it follows that areas closest to the source of flooding (i.e. edges) would sustain the longest periods of flooding. The flooding depth at each transect was measured using a four-foot (1.22 meters) wooden stake to which a strip of white construction paper of the same dimension was fitted. The suspended solids in the water stain the paper and leaves a mark after the tide recedes. The stakes were set at low tide on the same day in the center of the vegetation transect and read during the next tide cycle. Flooding duration was not measured; it was assumed that variations in depth would be an adequate indicator of variation in duration and can be inferred from height and distance from the source of tidal inflow. It has been observed that regions set far back from tidal source are the last to receive the flow of the tide (and thus the first to be exposed by its ebb), so that the flooding duration in these areas would be shorter than edge territories. All marsh wren nests were found to be at the edge (thus the stakes were likewise placed). It was also assumed that newly arrived males do not observe prospective sites for a long enough period to obtain an flood duration average either.

APPENDIX 3: DETERMINING THE CAUSE OF NEST FAILURE

Even well-constructed and ideally-sited nests can be destroyed by stochastic events, particularly violent storms, mammal predation, or conspecific nest destruction. Certain kinds of evidence is indicative of predation, but conspecific nest destruction is not always distinguishable from snake predation, therefore this type of nest failure was not separately analyzed. A nest was deemed predated if its contents have disappeared before fledgling is anticipated. If the nest is torn and the opening enlarged, this is usually a sign of predation by some mammal (Leonard and Picman 1987a, 1987b). If the nest is still in good condition, this could either mean conspecific destruction (Leonard and Picman 1987a) or snake predation (Roger Clapp, personal communication, July 1997). The other most common nest failure is destruction by storms, a frequent occurrence. A storm-battered nest is usually still intact, but askew and dislodged, and the cattail to which it is or was attached may be bent over or flattened. A nest was determined to be successful if at least one young fledged (Leonard and Picman 1987a).