

**HABITAT SELECTION, DISTRIBUTION, AND  
ABUNDANCE IN PURPLE MARTINS  
(PROGNE SUBIS)**

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## **DEDICATION**

This dissertation is dedicated first and foremost to my wonderful husband, Matt and our incredible son, Elliott. I could never have accomplished this without their sacrifices, love, support, and motivation. I love you both more than I have ever found the words to say to you.

To my mom, Kathleen Renee, who taught me that I could be both successful and a great mother through her amazing example.

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## TABLE OF CONTENTS

List of Tables .....	vi
List of Figures .....	ix
CHAPTER 1: INTRODUCTION .....	1
CHAPTER 2: AN INVESTIGATION OF THE FACTORS INFLUENCING PURPLE MARTIN (PROGNE SUBIS) HABITAT SELECTION .....	8
Methods.....	13
CV-ROC score .....	14
Results.....	14
Discussion .....	16
CHAPTER 3: AN INVESTIGATION OF THE FACTORS INFLUENCING PURPLE MARTIN (PROGNE SUBIS) DISTRIBUTION.....	32
Methods.....	36
PMCA data.....	36
BBS data .....	37
Climate and Land cover data .....	37
BRT models .....	38
CV-ROC score .....	39
Results.....	39
PMCA .....	39
BBS .....	40
Discussion .....	41
CHAPTER 4: AN EXAMINATION OF POPULATION TRENDS IN PURPLE MARTINS AND POTENTIAL COMPETITORS USING THE NORTH AMERICAN BREEDING BIRD SURVEY .....	56
Methods.....	62
The Data.....	62
The Analyses.....	62
Across Space .....	62
Over Time .....	63
Results.....	63
Across Space.....	63
Over Time .....	64
Discussion .....	66
CHAPTER 5: ESTIMATING NICHE OVERLAP OF PURPLE MARTINS AND TWO POTENTIAL COMPETITORS USING BOOSTED REGRESSION TREES .....	88
Methods.....	92
Abundance Criteria .....	93
Boosted Regression Tree Models .....	94

CV-ROC Scores.....	96
Results.....	96
Martins .....	96
Starlings .....	97
Sparrows .....	98
Niche Similarity .....	98
Discussion .....	99
Martins .....	100
Starlings .....	101
Sparrows .....	101
Evidence of Niche Overlap .....	102
CHAPTER 6: DISCUSSION.....	114
Appendix.....	120
Works Cited .....	176
Vita Auctoris.....	188

## LIST OF TABLES

Table 2.1	Published factors thought to positively impact martin nest site selection .....	22
Table 2.2	Published factors thought to negatively impact martin nest site selection .....	24
Table 2.3	Variables assessed at each nest site and how the variables were defined.....	25
Table 2.4	The contributions of the 18 predictor variables to the BRT model .....	27
Table 3.1	The 19 BIOCLIM variables used in the PMCA and BBS analyses .....	47
Table 3.2	Definitions of Land-cover classes.....	48
Table 3.3	Percent influence of predictor variables on the PMCA model .....	49
Table 3.4	Percent influence of predictor variables on the BBS model .....	50
Table 4.1	Correlations between average abundances from 1966-2003 across space .....	74
Table 4.2	Correlations between Eastern Bluebirds and Purple Martins in 5 years.....	75
Table 4.3	Correlations between Tree Swallows and Purple Martins in 5 years .....	76
Table 4.4	Correlations between House Sparrows and Purple Martins in 5 years.....	77
Table 4.5	Correlations between European Starlings and Purple Martins in 5 years.....	78
Table 4.6	Summary of mean abundances and significant population trends for all species..	79
Table 4.7	Summary of temporal population trends over 44 years for all five species.....	80
Table 4.8	Summary of temporal correlations on 30 routes over 44 years .....	81
Table A.1	Abundance data for birds on Alabama route 1 .....	120
Table A.2	Abundance data for birds on Alabama route 2 .....	121
Table A.3	Abundance data for birds on Alabama route 3 .....	122
Table A.4	Abundance data for birds on Delaware route 1 .....	124
Table A.5	Abundance data for birds on Delaware route 2 .....	126
Table A.6	Abundance data for birds on Delaware route 3 .....	128



Table A.7	Abundance data for birds on Georgia route 1 .....	130
Table A.8	Abundance data for birds on Georgia route 2 .....	131
Table A.9	Abundance data for birds on Georgia route 3 .....	133
Table A.10	Abundance data for birds on Georgia route 4 .....	135
Table A.11	Abundance data for birds on Indiana route .....	137
Table A.12	Abundance data for birds on Kentucky route 1 .....	138
Table A.13	Abundance data for birds on Kentucky route 2 .....	140
Table A.14	Abundance data for birds on Louisiana route .....	142
Table A.15	Abundance data for birds on Maryland route 1 .....	144
Table A.16	Abundance data for birds on Maryland route 2 .....	146
Table A.17	Abundance data for birds on Maryland route 3 .....	148
Table A.18	Abundance data for birds on Mississippi route .....	150
Table A.19	Abundance data for birds on Missouri route 1 .....	152
Table A.20	Abundance data for birds on Missouri route 2 .....	154
Table A.21	Abundance data for birds on New Jersey route .....	156
Table A.22	Abundance data for birds on North Carolina route .....	158
Table A.23	Abundance data for birds on Pennsylvania route .....	160
Table A.24	Abundance data for birds on Tennessee route 1 .....	162
Table A.25	Abundance data for birds on Tennessee route 2 .....	164
Table A.26	Abundance data for birds on Texas route 1 .....	166
Table A.27	Abundance data for birds on Texas route 2 .....	168
Table A.28	Abundance data for birds on Texas route 3 .....	170
Table A.29	Abundance data for birds on Virginia route 1 .....	172

Table A.30	Abundance data for birds on Virginia route 2 .....	174
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## LIST OF FIGURES

Figure 2.1	Single decision tree and its prediction surface from Elith et al. 2008 .....	28
Figure 2.2	Examples of crescent shaped exclusionary openings .....	29
Figure 2.3	Map of sites in Missouri and Illinois .....	30
Figure 2.4	Fitted function plots for the BRT model.....	31
Figure 3.1	A map of one year of housing locations obtained from the PMCA.....	51
Figure 3.2	Purple Martin breeding range map from PMCA .....	52
Figure 3.3	Breeding Bird Survey routes.....	53
Figure 3.4	Fitted function plots for the highest contributing variables in the PMCA model..	54
Figure 3.5	Fitted function plots of the highest contributing variables in the BBS model.....	55
Figure 4.1	Range map showing the distribution of Purple Martins .....	82
Figure 4.2	Locations of Breeding Bird Survey Routes .....	83
Figure 4.3	The distribution of correlations for Eastern Bluebirds and Purple Martins .....	84
Figure 4.4	The distribution of correlations for Tree Swallows and Purple Martins .....	85
Figure 4.5	The distribution of correlations for House Sparrows and Purple Martins .....	86
Figure 4.6	The distribution of correlations for European Starlings and Purple Martins.....	87
Figure 5.1	Range map showing the distribution of European Starlings.....	106
Figure 5.2	Range map showing the distribution of House Sparrows.....	107
Figure 5.3	The top three contributing variables for both models of martin presence .....	108
Figure 5.4	The top three contributing variables for both models of starling presence.....	109
Figure 5.5	The top three contributing variables for both models of sparrow presence.....	110
Figure 5.6	The top contributing factors to the low abundance models for all species.....	111
Figure 5.7	Overlaid contributions for mean temperature of the warmest quarter .....	112

Figure 5.8      The top three contributing factors to the high abundance models for species.....113

## CHAPTER 1: INTRODUCTION

The Purple Martin (*Progne subis*) is the largest North American swallow (Alderfer 2006). Martins are secondary cavity-nesters that breed colonially throughout much of North America and winter in South America. Five families of aerial insects make up the bulk of the diet: Coleoptera (Beetles), Hemiptera (True Bugs), Diptera (Flies), Hymenoptera (Bees and Wasps) and Lepidoptera (Butterflies) (Beal 1918; Johnston 1967). Historical nest sites consisted of holes in tree snags, saguaro cacti or in abandoned woodpecker holes (Allen and Nice 1952; Stutchbury 1991; Brown 1997; Alderfer 2006) and habitat preferences are thought to have been for open country, savanna, wooded marshes, and rural areas especially near water (Ehrlich et al. 1988; Brown 1997). A reduction in the number of natural nesting cavities and hypothesized competition for the remaining cavities are thought to have made martins almost entirely dependent on human-provided housing, nesting wherever adequate accommodations are located (Morton 1988; Stutchbury 1991; Brown 1997).

Martins have experienced regional population declines throughout the 20<sup>th</sup> century. While some analyses report a relatively stable North American breeding population over the last 40 years (Peterjohn et al. 1995; Tautin et al. 2008), more in depth consideration shows that the stability likely results from declines in one portion of the range that are offset by increases in another (Peterjohn and Sauer 1997). Peterjohn and Sauer (1997) report that, overall, Purple Martins have been experiencing a gradual decline in abundance since the 1980s particularly in the northern portion of their range and Tautin et al. (2008) reiterate that while martins are not declining range-wide, regionally there is cause for concern.

At least a dozen states and territories have listed the Purple Martin as “threatened”, “endangered”, or as a species of “special concern” (Airola and Grantham 2003; Hunt 2005; Tautin et al. 2008). In the first half of the 20<sup>th</sup> century, Allen and Nice (1952) describe declines throughout New England to the point of “near extermination” in the area. More recent reports confirm that the abundances of martins in Massachusetts (Clapp 2003), Rhode Island (Tautin et al. 2008) and New Hampshire (Hunt 2005) are decreasing and these martin populations are at risk of disappearing from these states all together. In the Midwest, martin abundances were found to be declining on 67% of the 422 Breeding Bird Survey routes (Herkert 1995). Population trends in Illinois and Indiana are also negative though non-significant (Tautin et al. 2008). Elsewhere, martin populations in Florida, Alabama, Michigan, Minnesota and Wisconsin have undergone significant decreases in abundance since the late 1960s (Tautin et al. 2008). Regional declines have also been reported in California (Airola and Grantham 2003; Alderfer 2006), Washington (Tautin et al. 2008) and British Columbia (Fraser 1997).

Martin population declines have been attributed to weather (Allen and Nice 1952; Brown 1997; Kramer and Hill 2002), habitat destruction (Finlay 1976; Campbell et al. 1997; Williams 1998) and competition for nest cavities (Allen and Nice 1952; Jackson and Tate 1974; Brown 1981; Ehrlich et al. 1988; Morton 1988; Clapp 2003). Abnormally high death rates have been seen in response to weather events like hurricanes (Robbins et al. 1986; Peterjohn and Sauer 1997) and martins have been described as particularly sensitive to bouts of cold weather (Brown 1997). Anecdotal local reports of martin deaths have been attributed to starvation linked to the impact of cold weather on the abundance of aerial insects, the martins main food source (Allen and Nice 1952; Brown 1981; Kramer and Hill 2002). As declines in martin populations have



occurred over a large geographic range and time period, it is unlikely that regional weather alone can account for the totality of declines seen in Purple Martins.

Habitat degradation has also been put forward to explain declines in Martin populations. In several other bird species including Violet-Green and Tree Swallows, nest cavities have been shown to be a limiting resource (Brawn and Balda 1988; East and Perrins 1988; Gustaffson 1988; Gutzwiller and Anderson 1988; Finch 1990; Bock et al. 1992). As dead trees that provided historical nesting sites for martins and other secondary-cavity nesters were removed, the number of available natural cavities declined (Hardin and Evans 1977; Munro and Rounds 1985).

Evidence that martins are being impacted by the removal of natural nesting sites is seen in the success of nest box projects. Martin declines in British Columbia and the Pacific Northwest have been reversed through the implementation of nest box projects. After the establishment of new nest boxes, Purple Martin abundances rebounded to their pre-decline numbers (Fraser 1997; Copley et al. 1999; Fraser et al. 1999a; Cousens et al. 2005b; Tautin et al. 2008). The success of regional nest box projects provides a powerful testament to the potential for martin conservation through the provision of artificial nest cavities and supports the hypothesis that habitat destruction is contributing to declines seen in martin local populations.

Competition for nest site cavities is the most-oft cited explanation for regional martin declines. However, empirical evidence for nest-cavity competition in this species is largely lacking. Competition with native Eastern Bluebirds (*Sialia sialis*) and Tree Swallows (*Tachycineta bicolor*) has been posited to occur based on a few anecdotal narratives (Allen and Nice 1952; Tate 1963; Jackson and Tate 1974). Exotic species such as European Starlings (*Sturnus vulgaris*) and House Sparrows (*Passer domesticus*) are also thought to compete with martins for cavities and competition with these species is thought to have been a major

contributor to martin declines. Evidence for competition with sparrows consists of reports of sparrows killing martin eggs and young (Barrows 1889), survey data showing that sparrows use martin housing (Jackson and Tate 1974), and the coincident timing of martin declines and sparrow appearance at sites (Morton 1988). For starlings, the evidence of a competitive interaction with martins is based again largely on anecdotes (Allen and Nice 1952; Morton 1988; Brown 1997). Brown (1981) does provide experimental data in support of competition occurring with starlings but his study was based on a relatively small sample size. However, more recently, Koenig (2003) found evidence that martin population sizes actually increased after the arrival of starlings. Therefore, the impact of competition on martins remains unclear and largely untested.

Much like the literature about competition, the literature on martin nest cavity preference is based largely on anecdotal reports. Morton (1988) asserts that martins prefer light-colored housing based on observing martins choose the white housing on his property over housing his neighbors had painted blue. There are also conflicting reports about whether martins prefer gourds (Morton 1988) or have no preference of gourds versus other types of housing (Layton 1969). Habitat characteristics such as proximity to water, distance from buildings, presence of wires or other perching sites and height of vegetation have all been hypothesized to influence martin nest box use (Jacobs 1905; Layton 1969; Fraser 1997; PMCA 2010), though these hypothesized influences remain untested. Further, many researchers assume that martins prefer wet habitats such as marshes and ponds attributing the preference to the abundance of the martins' food source, insects (Brown 1976; Finlay 1976; Zumeta and Holmes 1978; Brown 1981; Kramer and Hill 2002).

In this dissertation, I use a combination of fieldwork and modeling to investigate factors that affect habitat selection and the geographic distribution of Purple Martins. In Chapter 2, I use



local nesting data to examine factors influencing Purple Martin habitat selection. The data consist of 102 nesting sites throughout eastern Missouri and western Illinois that were monitored during late May and early June 2010. I recorded nest site characteristics and the presence of martins, starlings and sparrows during a standardized visit to each site. Boosted Regression Tree modeling was used to determine factors that are highly influential to martin presence and what the “preferred” conditions of those factors are.

In Chapter 3, I use both the Purple Martin Conservation Association (PMCA) and Breeding Bird Survey (BBS) datasets to examine factors influencing Purple Martin geographic distribution. For the PMCA dataset, I obtained a geo-referenced continental data set of martin presences and absences from the Purple Martin Conservation Association. The PMCA collects presence/absence data from citizen scientists who have set up martin housing on their property. Citizen scientists known as “landlords” use the PMCA’s website to report whether martins are present or absent at over 1,000 nest sites each year. The landlords report the location of the housing that they manage and whether it has martins. The PMCA provided me with their colony registration data for 2004-2008. The organization is collecting this data in an effort to locate all active and inactive martin colonies throughout North America (PMCA 2010).

The BBS is a long-term citizen science data collecting effort that records bird species abundances across the United States and Canada (Bystrak 1981). The BBS was developed in order to monitor bird populations over a large geographic area. Volunteers record all birds seen or heard within a 400 m radius during a three minute point count. Point counts are conducted every 800 m along 3,229 routes within the contiguous United States (see Fig. 3.3). Routes are 39.2 km long and the same routes are surveyed each year. The survey is conducted during the

height of the breeding season every year and began in 1966. Data collected by survey volunteers is available via the BBS website ([www.pwrc.usgs.gov/bbs/](http://www.pwrc.usgs.gov/bbs/)).

I use both datasets to build BRT models and determine what factors are highly influential to martin presence. I compare the results of models built using both datasets and comment on possible reasons for differences. There is a critical difference in the extent of the two datasets: the PMCA data contains presence/absence points only from within the Purple Martin's known geographic range while the BBS dataset contains presence/absence points both within and outside the martin's range.

In Chapter 4, I examine the competition hypothesis for explaining regional martin declines. I use the BBS abundance data for Purple Martins, Eastern Bluebirds, Tree Swallows, House Sparrows and European Starlings to examine population trends in these species and investigate competition between martins and the other species included using spatial and temporal correlation analyses. Competition predicts negative correlations between species pairs across space and over time (Toft et al. 1982; Hastings 1987; Wooten 1987; Tilman 1999). I use both 37-year average abundance on BBS routes and individual year abundances to investigate spatial co-occurrence. I then use abundance data for martins and their competitors on 30 routes of high martin abundance to investigate patterns and population trends for all five species over time.

In Chapter 5, I use the BBS datasets for Purple Martins, House Sparrows and European Starlings to estimate niche overlap in these species as a method for considering possible competition between them. If competition is occurring between these species as proposed, I would expect the species' BRT models to have the same highly influential factors. I use two different abundance criteria in order to consider possible differences in niche models created

using all possible presence points and models created using only high abundance presence points. I use similarity in factors affecting BRT models for the three species in order to comment on possible competition under both abundance criteria.

In Chapter 6, I summarize my findings regarding factors that affect Purple Martin habitat selection, geographic distribution and abundance. I highlight the importance of considering scale, data extent and abundance in Species Distribution modeling and summarize future directions for research to build on the results of my dissertation.

## **CHAPTER 2: AN INVESTIGATION OF THE FACTORS INFLUENCING PURPLE MARTIN (PROGNE SUBIS) HABITAT SELECTION**

Habitat selection by animals is based on a number of different factors. Because of their vagility birds have a particularly high potential to select habitats that yield high fitness (Cody 1985). In birds, climate, land cover, previous experience in a habitat, food availability, nest site availability, competition, conspecific attraction, and philopatry affect habitat selection (Cody 1985; Jones 2001).

Habitat selection is often studied through observation of individual or population decisions on where to settle, breed, roost or forage. Historically, empirical studies of habitat selection have relied on correlations between habitat characteristics and the spatial distribution of the animal species (Jones 2001; Guisan and Thuiller 2005). Two different strategies have typically been employed in order to conduct these empirical studies. In the first methodology, ecologists compare fitness in two different environments in order to make predictions about characteristics of preferred habitat (Rosenzweig 1991). In the second method, habitat characteristics in occupied versus non-occupied habitat are compared or alternatively, comparisons are made between occupied and available habitat in order to determine what factors or characteristics influence presence (Gilmer et al. 1975; Jones 2001). The latter approach has been criticized because it is based on arbitrary assessments of availability (Johnson 1980). Often habitat use in these studies is assessed using radio-tracking of individuals. Analyzing radio-tracking data provides some difficulties such as data pooling (combining data from individual animals), determining appropriate sampling level (individual, population, etc.) and determination of habitat availability (Aebischer et al. 1993). Equating movement through a habitat type with selection of that habitat or a preference for habitat type/features may also not be appropriate if



usage and availability are not properly defined (Johnson 1980; Aebischer et al. 1993). Radio-sampling data also provides only a subsample of animal behavior (Aebischer et al. 1993).

Another strategy for determining preference for habitat characteristics is to census study sites along a habitat gradient, such as riparian habitat ranging from open fields to closed-canopy woodland, in order to determine a preference for habitat type (Stauffer and Best 1980). One of the drawbacks of this approach is that experimenters must determine ahead of time which features of a habitat might be most important to habitat selection in order to census the proper gradient (Austin 2007) and availability must be assessed are often based on subjective designations (Johnson 1980). For example, studies of habitat selection in cavity nesting birds have been inconclusive because of the failure to incorporate a sufficient range of habitat characteristics, or because the nest sites surveyed were not established specifically to assess habitat selection in these birds (Horn et al. 1996).

Recently an alternative method has been developed to determine which factors influence habitat selection that utilizes a subset of niche modeling analyses called species distribution models (SDMs) which incorporate both climate and other abiotic factors of the habitat. SDMs use the features of habitats which a species occupies and the features of habitats where the species is not found to identify factors that may be important in determining where a species can survive or how a species chooses a habitat. Commonly applied SDMs include Generalized additive models (GAMs), Generalized linear models (GLMs) and machine learning models such as MaxEnt, a maximum entropy algorithm and GARP, an integrated spatial analysis program used to predict species distributions. However, the performance of these types of SDMs has been called into question (Pearson and Dawson 2003; Elith and Graham 2009). GAMs, GLMs and MaxEnt are predictive SDMs that identify contributing factors but often perform poorly and

cannot analyze categorical and continuous data simultaneously. And recent evidence indicates that these models, which are often developed using data from a broad geographical scale (Guisan and Thuiller 2005), may not predict well at local scales (Trumbo et al. 2011).

Recent advances have resulted in an application of boosted regression analyses to SDM niche modeling called Boosted Regression Tree (BRT) analyses (De'ath and Fabricius 2000; Elith et al. 2006; Elith et al. 2008). BRT analyses use records of species presences and absences to build niche models using decision trees or binary splits of the data (Fig. 2.1) combined with boosting, a method for aggregating many simple models into a more complex model (Elith et al. 2008). The BRT then provides the data on how predictive the overall model is by testing it using the 10% of the data that was not used to build the model, resulting in a Cross-Validation Receiver Operating Curve (CV-ROC) score. Combining decision trees using boosting enhances predictive performance (Elith et al. 2008). BRTs have the advantage of being able to combine data of different types such as continuous and categorical variables collected on different scales and can utilize large numbers of variables more effectively than other modeling methods (Elith et al. 2008). The relative contribution or influence of predictor variables on the model are determined using measures based on the number of times a variable is used for splitting, weighted by how much that split improves the model, averaged over all the trees included in the model and scaled so that sum of all the relative contributions of the variables to the model equals 100 (Friedman 2001; Friedman and Meulman 2003).

Here, I use BRTs to investigate habitat selection in Purple Martins (*Progne subis*), a colonial bird that breeds throughout much of North America. Historically, these birds nested in abandoned woodpecker cavities and holes in cacti (Stutchbury 1991). Competition for nest sites with the introduced European Starling (*Sturnus vulgaris*) and House Sparrow (*Passer*

*domesticus*) are thought to have impacted the abundance of Purple Martins in their historical range (Copley et al. 1999). A combination of human habitat alteration and competition has rendered the Purple Martin almost entirely dependent on human-provided housing (Allen and Nice 1952; Jackson and Tate 1974; Morton 1988; Stutchbury 1991). Declines in Purple Martin populations were documented in the late 1960s and early 1970s (Higman 1944a; Mayfield 1969) and nest box projects have been successful in helping the population numbers to rebound (Fraser 1997; Copley et al. 1999). Since martins are so reliant on nest boxes, I assess nest box occupancy and surrounding factors that influence nest box use. Similar studies have been conducted in Eastern Bluebirds (*Sialia sialis*), another cavity-nesting species largely reliant on human-provided housing, in order to try and clarify habitat characteristics important to the birds (Willner et al. 1983; Horn et al. 1996). Prior to these studies of bluebird nest box use, much of what was known about bluebird habitat selection was anecdotal, inconclusive or contradictory as is the case currently for Purple Martins.

Many factors have been hypothesized to influence nest box use, or habitat selection, by Purple Martins including aspects of the nest cavity as well as vegetation structure nearby. Some of the variables thought to positively impact nest box use include presence of exclusionary openings meant to deter competitors, urbanization of the nest site location and proximity to water (see Table 2.1 for a more complete list) (Kermode 1923; Johnston and Hardy 1962; Jackson and Tate 1974; Finlay 1976; Brown 1981; Campbell et al. 1997; Fraser 1997; Kramer and Hill 2002). Some of the variables thought to negatively impact martin nest box use include dark color of nest cavities, proximity of trees, presence of buildings within 9m or more than 36.5m away (see Table 2.2 for a more complete list) (Kermode 1923; Johnston and Hardy 1962; Jackson and Tate 1974; Finlay 1976; Brown 1981; Campbell et al. 1997; Fraser 1997; Kramer and Hill 2002). Other nest

site characteristics such as nest box color and number of nesting compartments have also been hypothesized to influence preference for nesting locations. Several researchers suggest that martins prefer white houses (Jacobs 1905; Layton 1969; Morton 1988) and that they prefer at least six nesting compartments (Fraser 1997). Layton (1969) states that martins have no preference for houses over gourds or vice versa. Height of the housing and presence of predator guards are also reported to be influential in martin habitat selection (Jacobs 1905; Layton 1969; Fraser 1997; PMCA 2010). Habitat characteristics such as proximity to water, distance from buildings, presence of wires or other perching sites and height of vegetation have all been hypothesized to influence martin nest box use (Jacobs 1905; Layton 1969; Fraser 1997; PMCA 2010). Others have reported that Purple Martin housing should be placed in open areas with no overhanging trees (Jacobs 1905; Layton 1969; Mayfield 1969; Fraser 1997; PMCA 2010). However, much of the information regarding nest box design, placement and success at recruiting martins remains anecdotal (Allen and Nice 1952; PMCA 2010).

Several studies and reports about martins suggest that competition for housing with European Starlings (*Sturnus vulgaris*) and House Sparrows (*Passer domesticus*) is important in determining nest box use (Kermode 1923; Mayfield 1969; Jackson and Tate 1974; Brown 1981; Morton 1988; Campbell et al. 1997; Doughty and Fergus 2002). As competition is believed to be responsible in part for the almost complete dependence of martins on human-provided housing, it is important to determine what influence these competition related factors may have on housing use. Jackson and Tate (1974) showed that higher vegetation height seemed to favor sparrows while lower vegetation height around the houses appeared to favor martins offering a possible explanation for why vegetation height may be important through reduced competition. Many commercially available martin houses and gourds are now equipped with exclusionary openings