BREEDING BIOLOGY AND HABITAT ASSOCIATIONS OF THE

ALTAMIRA ORIOLE AND NORTHERN BEARDLESS-TYRANNULET

IN THE LOWER RIO GRANDE VALLEY, TEXAS

A Thesis

by

SCOTT MICHAEL WERNER

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2004

Major Subject: Wildlife and Fisheries Sciences

BREEDING BIOLOGY AND HABITAT ASSOCIATIONS OF THE

ALTAMIRA ORIOLE AND NORTHERN BEARDLESS-TYRANNULET

IN THE LOWER RIO GRANDE VALLEY, TEXAS

A Thesis

by

SCOTT MICHAEL WERNER

Submitted to Texas A&M University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Approved as to style and content by:

Sallie J. Hejl	R. Douglas Slack
(Co-Chair of Committee)	(Co-Chair of Committee)
Fred E. Smeins	Robert D. Brown
(Member)	(Head of Department)

August 2004

Major Subject: Wildlife and Fisheries Sciences

ABSTRACT

Breeding Biology and Habitat Associations of the Altamira Oriole and

Northern Beardless-Tyrannulet in the Lower Rio Grande Valley, Texas. (August 2004)

Scott Michael Werner, B.S., University of California, Santa Barbara

Co-Chairs of Advisory Committee: Dr. Sallie J. Hejl
Dr. R. Douglas Slack

I studied the breeding biology and nesting ecology of the Altamira Oriole

(*Icterus gularis*) and Northern Beardless-Tyrannulet (*Camptostoma imberbe*), two

songbirds inhabiting remnant tracts of Tamaulipan brushland of the Lower Rio Grande

Valley, Texas during 2002-2003. I found 76 active oriole nests, 7 of which were reused

for second broods, for a total of 83 nesting attempts. I estimated that nearly 20% of the

oriole breeding population were subadult, or second-year orioles, which is extremely

rare for this species. Oriole breeding pairs were found in high densities and may be at

their highest level at the study sites since the 1970s. Fifty-nine percent of oriole nests

fledged, and 37% failed. Six nests produced Bronzed Cowbird (*Molothrus aeneus*)

fledglings. Vegetation analysis suggests that orioles prefer the tallest trees at the sites in

which to place their nests. A greater number of fallen logs near the nest was also a

predictor of nest sites, which suggests that orioles prefer scattered woodlands, but also

that many of the forests probably continue to shift to a more open, thorn-scrub climax

stage. I monitored 28 Northern Beardless-Tyrannulet nests, which were restricted to a

smaller number of study tracts than Altamira Orioles. Historical records are lacking for

Northern Beardless-Tyrannulets at these sites, but my surveys indicated that there were

similar seasonal numbers of tyrannulets at some of the study sites as there were during 1996-1998. Forty-three percent of nests were successful and 57% failed. Higher abundances of epiphytic Spanish moss (Bromeliaceae: *Tillandsia usneoides*) and ball moss (Bromeliaceae: *Tillandsia recurvata*) were the most important predictors of nest sites. The continued existence of these two species in South Texas will depend upon the preservation of tall forests, and in the case of the tyrannulet, forests rich in *Tillandsia* epiphytes.

DEDICATION

This thesis is dedicated to my family: Dad, Mom, and Angela, and to my partner, Veronica. You have all encouraged me and stuck by me in everything I have done. This thesis has also taken time away from spending more time with you, and I want to express my gratitude and love to all of you.

ACKNOWLEDGEMENTS

Finally, I would like to thank all of my friends back home for their support, and friends and colleagues at Texas A&M University for helping me through the process.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

BACKGROUND

During the last 100 years or more, populations of many migratory and non-migratory

bird species have decreased across North America (e.g., Terborgh 1992, Vickery et al.

1999). Habitat destruction and fragmentation are the leading causes of many population

declines, and songbirds may be more prone to local extinction events than other taxa

(Diamond 1984, Robinson et al. 1995). One aspect of conservation biology is to study

how avian species use degraded or fragmented landscapes, so that we can manage for

'good' habitats that will be beneficial to a species' long-term survival (Robinson et al.

1995). Because every species is different, and because different regions of the continent

have unique conservation threats, intensively studying and monitoring individual avian

populations to elucidate the limiting factors of population growth will be the best way to

prepare conservation plans that work. For example, the international Partners in Flight

group is taking a continent-wide look at which species are most at risk with its North

American Landbird Conservation Plan, but is also promoting its regional bird

conservation plans as the most effective way to pool resources and effect conservation

measures for individual populations (Pashley et al. 2000, Rich et al. 2004).

Tropical avifaunas are incredibly diverse but have been little-studied relative to

birds in the United States. The conservation of these species requires basic knowledge

_____

This thesis follows the style and format of Condor.

about their life history strategies and reproductive ecologies, information that is lacking for many species. Two tropical avian species whose ranges extend into the United States, but whose long-term population status in the United States is uncertain, are the Altamira Oriole (*Icterus gularis*) and the Northern Beardless-Tyrannulet (*Camptostoma imberbe*). Little is known about these birds, but much of their former habitat in the Lower Rio Grande Valley (LRGV) of deep South Texas has been destroyed. Knowledge of their breeding ecologies and habitat affinities will allow for more appropriate conservation measures, and ultimately, for their persistence as inhabitants of the United States.

The U.S. Geological Survey has designated nine LRGV landbird species, including the Northern Beardless-Tyrannulet and Altamira Oriole, as immediate research priorities in its Species At Risk program (U.S. Geological Survey 2000; Table 1). Of these nine, the most appropriate candidates for a nesting study in the LRGV are Altamira Oriole and Northern Beardless-Tyrannulet because they are the two most-abundant and easily studied locally nesting birds of the nine.

OBJECTIVES

My objectives in this study were to assess past population trends and current breeding status and distribution, determine nesting success and the limiting factors of nesting success and productivity, and investigate nest-site selection parameters for the Altamira Oriole and the Northern Beardless-Tyrannulet in the LRGV.

Table 1. Priority South Texas landbirds in the Species At Risk program (U.S. Geological Survey 2000).

Common name	Scientific Name
Red-billed Pigeon	*Columba flavirostris*
Ferruginous Pygmy-Owl[a]	*Glaucidium brasiliensis*
Buff-bellied Hummingbird	*Amazilia yucatanensis*
Northern Beardless-Tyrannulet[a]	*Camptostoma imberbe*
Rose-throated Becard[a]	*Pachyramphus aglaiae*
Tropical Parula[a]	*Parula pitiayumi*
Botteri's Sparrow	*Aimophila botterii*
Altamira Oriole	*Icterus gularis*
Audubon's Oriole	*Icterus graduacauda*

[a] Listed as threatened on the State of Texas List of Threatened and Endangered Species (Campbell 1995).

CHAPTER II

STUDY AREA

The Lower Rio Grande Valley of Texas is a unique biotic area that Blair (1950) recognized and called the Matamoran Biotic District. It supports a rich collection of flora and fauna not found elsewhere in the Tamaulipan Biotic Province of southern Texas and northeastern Mexico. The Rio Grande historically drained its 472,000 km^2 basin through the coastal plain, supporting a mosaic of river channels and uplands with abundant plant and animal life (U.S. Fish and Wildlife Service 1997, Texas Natural Resource Conservation Commission 2002). The biotic communities of the LRGV are the product of the convergence of coastal, desert, and tropical and subtropical environments (Clover 1937, Blair 1950). The proximity of the Sierra Madre to the west creates a funneling effect for migratory birds traveling along the Mississippi and Central Flyways (Shackleford et al. 2000).

Because of its fertile soils, the Lower Rio Grande Valley (consisting of Cameron, Willacy, Hidalgo, and Starr counties) has been heavily modified by human settlement. Since the 1920s, when mechanized farming began to heavily modify the LRGV plain, more than 95% of the native vegetation cover has been removed, resulting in the few present-day 'islands' of native plant and animal life (Jahrsdoerfer and Leslie 1988). Water diversions and dams have prevented the recent flooding of the river, especially since Falcon Dam was completed in 1953, and the seasonal flooding from the Rocky Mountains and elsewhere in the watershed is not a part of the delta system anymore

(Gehlbach 1981, U.S. Fish and Wildlife Service 1997). Since the North American Free Trade Agreement was ratified in 1994, trade and urbanization in the LRGV have greatly increased (Texas Natural Resource Conservation Commission 2002).

The U. S. Fish and Wildlife Service (USFWS) has begun to establish a continuous corridor of native vegetation stretching along the 443 km of river from Falcon Dam to the Gulf of Mexico that will eventually cover 53,418 ha within the Lower Rio Grande Valley National Wildlife Refuge (LRGVNWR; U.S. Fish and Wildlife Service 1997). Currently, about 35,630 ha of land are protected within the LRGVNWR. Santa Ana National Wildlife Refuge comprises 853 ha along the Rio Grande and is within the geographic area covered by the LRGVNWR tracts. Laguna Atascosa National Wildlife Refuge covers 18,211 ha along the coast, and is an important component of the planned corridor. The corridor effort will involve purchasing the few remaining small parcels of native brush as well as purchasing and restoring large areas of farmland to native vegetation cover.

To study the breeding ecology of the Altamira Oriole and Northern Beardless-Tyrannulet, I surveyed the following pieces of land in Hidalgo County, listed in downstream to upstream order (Figure 1; Table 2):

(1) Santa Ana National Wildlife Refuge (Santa Ana). This is the largest tract of native thorn woodland remaining in the LRGV. It has elements of Mid-Delta Thorn Forest characterized by tall Texas ebony (*Chloroleucon ebano*), anacua (*Ehretia anacua*), and brasil (*Condalia hookeri*), as well as Mid-valley Riparian, dominated by cedar elm (*Ulmus crassifolia*), sugar hackberry (*Celtis laevigata*), and Mexican ash
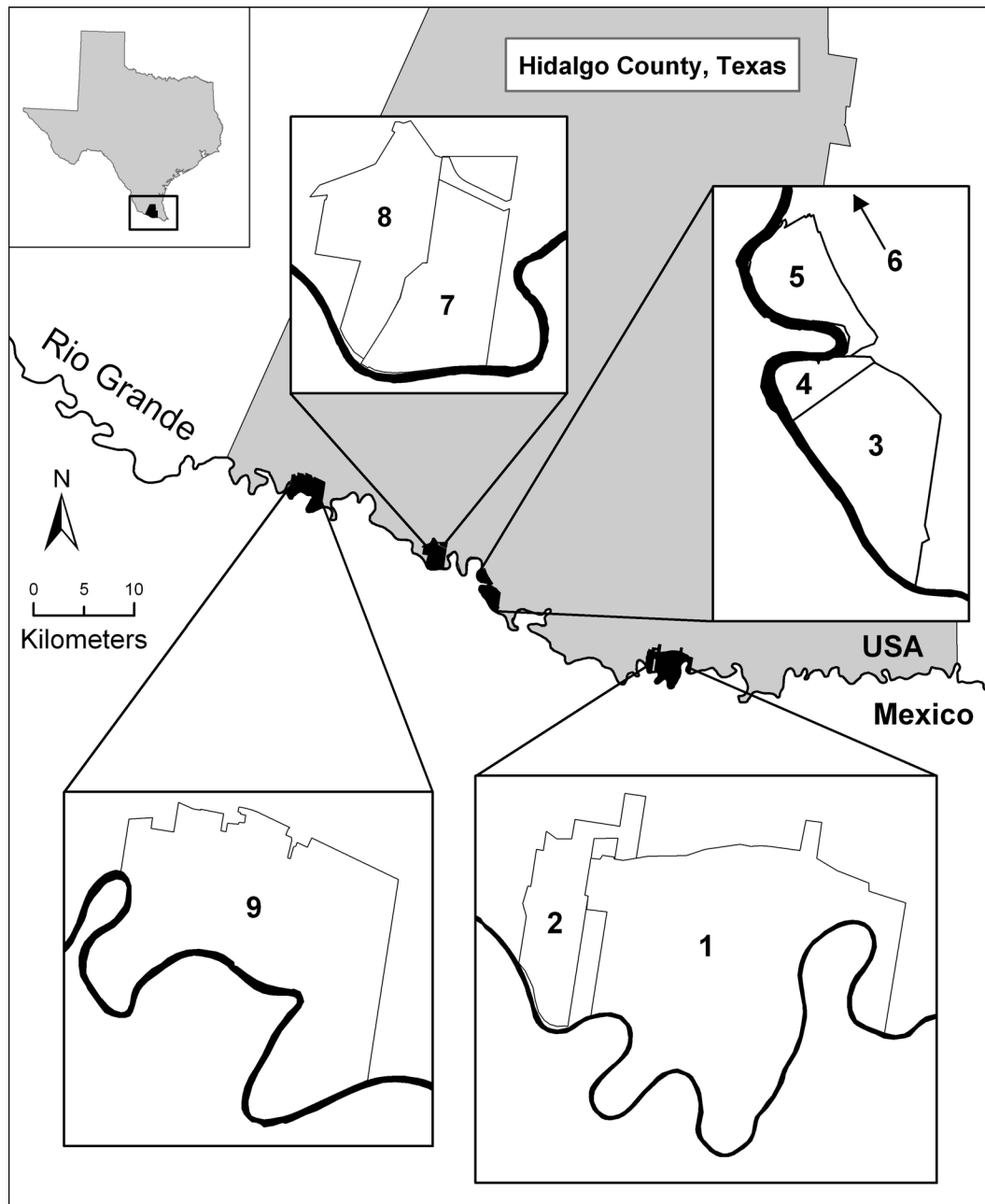
Figure 1. Map of tracts surveyed for nests of Altamira Orioles and Northern Beardless-Tyrannulets in Hidalgo County, Texas, during 2002-2003. From downstream to upstream, tracts are (1) Santa Ana National Wildlife Refuge, (2) Marinoff tract, Lower Rio Grande Valley National Wildlife Refuge (LRGVNWR), (3) Gabrielson tract, LRGVNWR, (4) Anzalduas County Park, (5) Madero tract, LRGVNWR, (6) Madero residential, (7) El Morillo Banco tract, LRGVNWR, (8) Bentsen-Rio Grande Valley State Park, (9) La Joya tract, LRGVNWR.

Table 2. Tracts surveyed and approximate areas searched for nests of Altamira Oriole and Northern Beardless-Tyrannulet in Hidalgo County, Texas, 2002-2003. List is ordered from downstream to upstream.

Name	Lat/Lon	Size (ha)	Area Searched 2002	Area Searched 2003	Landowner/administrator
Santa Ana National Wildlife Refuge	98°9'W, 26°4'N	853	30%	50%	U.S. Fish and Wildlife Service
Marinoff tract, LRGVNWR[a][b]	98°10'W, 26°4'N	171	90%	50%	U.S. Fish and Wildlife Service
Gabrielson tract, LRGVNWR	98°19'W, 26°8'N	264	5%	10%	U.S. Fish and Wildlife Service
Anzalduas County Park	98°20'W, 26°8'20"N	49	100%	100%	Hidalgo County
Madero tract, LRGVNWR	98°20'W, 26°9'N	122	30%	50%	U.S. Fish and Wildlife Service
Madero residential[b]	98°20'W, 26°10'N	42	0%	50%	private
El Morillo Banco tract, LRGVNWR	98°22'30"W, 26°10'N	262	80%	90%	U.S. Fish and Wildlife Service
Bentsen-Rio Grande Valley State Park	98°23'W, 26°10'N	238	100%	100%	Texas Parks and Wildlife
La Joya tract, LRGVNWR	98°30'W, 26°13'N	771	10%	10%	U.S. Fish and Wildlife Service

[a] LRGVNWR - Lower Rio Grande Valley National Wildlife Refuge
[b] Marinoff and Madero Residential were surveyed primarily by vehicle.

(*Fraxinus berlandieriana*) mixed with mesquite (*Prosopis glandulosa*) and granjeno (*Celtis pallida*; Jahrsdoerfer and Leslie 1988). The two major habitat types mix extensively, creating thorn forest, thorn scrub, bottomland or riparian forest, and scattered deciduous thorn woodland.

Santa Ana has remained relatively undisturbed since its acquisition in 1943 and has an active water management program that floods several large wetlands in the northern and western portions of the refuge and a large resaca, or former river channel, in the southern part of the refuge. Approximately 9.5 km of the Rio Grande flows along the southern edge of the refuge. After Falcon Dam's completion in 1953, the refuge flooded naturally from hurricanes in 1958, 1967, and 1971 (Gehlbach 1981). Santa Ana is almost completely surrounded by agriculture in the United States and on the Mexican side of the river.

(2) Marinoff tract, LRGVNWR (Marinoff). Marinoff abuts Santa Ana to the west and is largely regrowth with scattered woodlands. Marinoff was not as thoroughly searched as Santa Ana (Table 2).

(3) Gabrielson tract, LRGVNWR (Gabrielson). The vegetation of Gabrielson closely resembles that of Santa Ana, with tall, riparian forest, thorn forest, and upland thorn scrub. Spanish moss (*Tillandsia usneoides*) and ball moss (*Tillandsia recurvata*) are abundant at Gabrielson, like Santa Ana. Gabrielson is near a major floodway, and Anzalduas dam creates a small lake that likely provides subsurface moisture to the small resaca in the northwestern corner of Gabrielson. Future threats to Gabrielson include a new U.S.-Mexico bridge that could begin construction as soon as 2004 on the eastern

side of the tract. The port of entry, however, will be located farther north in the town of Granjeno.

(4) Anzalduas County Park. Adjacent to the Anzalduas Diversion Dam, which was completed in 1960, Anzalduas County Park supports a tall forest with abundant *Tillandsia* similar to Gabrielson, but the understory has been removed to make room for picnic grounds and other recreational events. Several rare South Texas birds have nested in the park recently, including Gray Hawk (*Asturina nitida*) and Rose-throated Becard (*Pachyramphus aglaiae*; T. Brush, University of Texas – Pan American, unpubl. data).

(5) Madero tract, LRGVNWR (Madero). Madero is across the floodway from Anzalduas County Park and Gabrielson. Although most of the tract is upland scrub, there are several patches of tall thorn forest and bottomland forest along the Rio Grande and, to a smaller extent, along a canal on the east side of the tract.

(6) Madero residential. This small suburban development near the Rio Grande is just north of Madero tract and consists of a variety of tall native and ornamental vegetation interspersed among the houses. The site is within Mission city limits but is located about 2 km south of other developments in the town, separated by agricultural fields. This site was surveyed during 2003 only.

(7) El Morillo Banco tract , LRGVNWR (El Morillo Banco). This tract is mostly reclaimed farmland that was replanted in the early 1990s with native vegetation. A key landscape feature here is the large resaca that forms part of the boundary with Bentsen State Park, which is the adjacent parcel to the west. Although dry during this study, the

resaca supports long strips of riparian vegetation dominated by cedar elm and sugar hackberry and used by many bird species.

(8) Bentsen-Rio Grande Valley State Park (Bentsen). Bentsen and El Morillo Banco have much drier soils that sites downstream mentioned above. But Bentsen does support small patches of thorn forest and bottomland forest along several ancient river channels. Unfortunately, Bentsen's dense forest patches are drying out and shifting to a more open, thorny woodland dominated by mesquite, which is used by birds differently than the moister forest types.

(9) La Joya tract, LRGVNWR (La Joya). La Joya is at the upper end of the delta and the densest forest habitat is found on accretions along the Rio Grande. Much of the tract was replanted in the early 1990s over former farmland, and some of the restored areas of huisache (*Acacia minuata*) and tepeguaje (*Leucaena pulverulenta*) have grown tall over the past 10 years. Few if any *Tillandsia* epiphytes are found at this site.

CHAPTER III

NESTING SUCCESS AND NEST-SITE SELECTION

OF THE ALTAMIRA ORIOLE

INTRODUCTION

The Lower Rio Grande Valley of Texas (LRGV) supports a highly diverse flora and

fauna and represents the northernmost range limit of many tropical species (Clover 1937,

Blair 1950, Oberholser 1974, Jahrsdoerfer and Leslie 1988).   Since the 1920s the LRGV

(consisting of Cameron, Hidalgo, Willacy, and Starr counties) has undergone a massive

landscape transformation from a mosaic of subtropical evergreen forest, riparian

woodland, and chaparral (collectively referred to as Tamaulipan brushland) to

agricultural fields and urban developments. An estimated 95% or more of the original

native brushland habitat in the LRGV has been cleared, and estimates are nearly as high

for adjacent Tamaulipas, Mexico (Marion 1974, Jahrsdoerfer and Leslie 1988). Since

major flooding was eliminated in 1953 with the completion of Falcon Dam, plant

communities in some protected areas have shifted from subtropical evergreen forest to

shorter, denser, thorn forest and thorn scrub, accompanied by shifts in avian

communities (Gehlbach 1987, Brush and Cantu 1998). Local plant communities have

also been affected by severe freezes and droughts (Lonard and Judd 1991, Eddy and

Judd 2003).

Jahrsdoerfer and Leslie (1988) identified 67 LRGV vertebrate species on the

state and federal lists of threatened and endangered species. Several authors have

studied distributions of LRGV avian species (e.g., Sennett 1878, Davis 1940, Gehlbach 1987, Brush 1998b, Brush 1999) but data are lacking regarding rates of breeding success, productivity, and even general life history attributes of many species (e.g., Brush 1998a). Abundance indices cannot necessarily tell us if we are managing for the appropriate habitat features (Van Horne 1983), and a highly fragmented landscape such as the LRGV could contain source and sink habitats with highly variable recruitment rates (Pulliam 1988). Therefore, identifying the habitat features that affect productivity is essential if we want to manage for self-sustaining bird populations (Martin 1992).

Populations of the Altamira Oriole, a year-round resident of the LRGV, have recently declined, and this species is on the Texas Organization for Endangered Species watch list as potentially threatened or endangered in the United States (Texas Organization for Endangered Species 1995). The Altamira Oriole is listed by Partners in Flight as moderately high priority conservation status, and the U.S. Geological Survey has identified the Altamira Oriole as one of nine LRGV landbirds needing immediate research attention in its Species At Risk program (Pashley et al. 2000, U.S. Geological Survey 2000; Table 1).

The Altamira Oriole inhabits subtropical and tropical lowland forests from the LRGV southward throughout much of Mexico and into Nicaragua (Dickey and van Rossem 1938, Sutton and Pettingill 1943, Skutch 1954, American Ornithologists' Union 1998). It builds a large (often > 50 cm long), conspicuous, pendulous nest in semi-open forests and riparian woodlands. The nest is usually placed in large trees 4-15 m above the ground or surface of the water, and can often be seen from a distance. Because it is

placed on the tip of a small flexible branch, the nest is thought to be inaccessible to many predators (Sutton and Pettingill 1943).

The Altamira Oriole was not known to nest in the LRGV until 1951, although birds were previously seen on Audubon Christmas Bird Counts (Sennett 1878, Smith 1910, Friedmann 1925, Grimes 1953, Oberholser 1974). From the 1950s until the 1980s Altamira Oriole populations in the LRGV increased, while Hooded Oriole (*Icterus cucullatus*) and Audubon's Oriole (*Icterus graduacauda*) populations decreased, presumably due to habitat destruction and heavy nest parasitism by Bronzed Cowbirds (*Molothrus aeneus*; Oberholser 1974, Gehlbach 1981, Carter 1986). Today Hooded Orioles are virtually absent from stands of native brush in the LRGV (Brush 2000b, S. M. Werner, personal observation) and Audubon's Orioles are very rare and restricted to the far west end of the LRGV (Brush 2000a). Altamira Orioles may have avoided high levels of nest parasitism because of the pendulous nest and the fact that they are capable of ejecting cowbird eggs (Hathcock 2000). Numbers of Altamira Oriole nests at Santa Ana, the largest native brush tract left in the LRGV, peaked in the early 1970s at 35 nests (Webster 1972), but this population slowly declined until 1990-1994, when fewer than four nests were found each year (Brush 1998a). However, a breeding population of 20-25 pairs in the riparian forest below Falcon Dam during 1994-1996 appeared stable (Brush 1998a). By the late 1990s Altamira Orioles appeared to have made a slight rebound at Santa Ana when six to nine breeding pairs per year were estimated during 1997-1999 (Hathcock and Brush 2004).

Continued habitat degradation is presumed to be the leading cause of decline of the Altamira Oriole, although few data exist about breeding success, levels of nest predation and parasitism, foraging requirements, and overwinter survival (Brush 1998a). Basic information, such as the length of the incubation and nestlings stages, was unknown because of the inaccessibility of nests, but Hathcock (2000) was able to investigate nesting success and stage length with the aid of a micro-video camera. The first confirmed report of Altamira Orioles raising Bronzed Cowbirds was in 1996 (Brush 1998a), and Hathcock (2000) observed Altamira Orioles ejecting cowbird eggs as well as raising Bronzed Cowbirds. No studies have addressed detailed habitat preferences for nest-site selection, but the presence of tall trees with an available branch on the northwestern side (so the tree can shield the nest from prevailing southeasterly winds) appears to be a major preference (Brush 1998a, Hathcock 2000).

In this study my objectives were to (1) assess the current and past Altamira Oriole nesting status on the largest riparian brush tracts in the LRGV, (2) describe nesting phenology and determine rates of nesting success and differences among study sites, (3) examine the limiting factors of nesting success and productivity, and (4) describe nest-site selection.

METHODS

STUDY AREA

I conducted all nest monitoring during 2002 and 2003. During July and August 2001, I chose most of the study sites by finding areas that supported large numbers of orioles, or that otherwise had recent records of nesting. All study sites were located in Hidalgo

County, Texas, which is considered to be in the "Mid-Valley" of the LRGV (Figure 1).

Climate is semi-arid and subtropical (Jahrsdoerfer and Leslie 1988) with an average

yearly rainfall of 56 cm and average high temperatures exceeding 35 C° in August. The

Mid-Valley shows a bimodal yearly rainfall pattern. September is the wettest month,

with 103 mm rainfall, and May and June each receive about 71 mm of rain (1961-2001

averages; National Climatic Data Center 2003).

Vegetation at the study sites has been characterized as "Mid-valley Riparian

Woodland" and "Mid-delta Thorn Forest" (Jahrsdoerfer and Leslie 1988). Ancient

floodways, or resacas, alternating with upland areas supported a mosaic of plant

communities within the sites. Some dry resacas with little standing water contained

bottomland forests composed of large Mexican ash (*Fraxinus berlandieriana*), cedar elm

(*Ulmus crassifolia*), and sugar hackberry (*Celtis laevigata*) trees. Upland and transition

areas supported drier thorn forest and thorn scrub, consisting of Mexican ash, cedar elm,

sugar hackberry, anacua (*Ehretia anacua*), Texas ebony (*Chloroleucon ebano*),

tepeguaje (*Leucaena pulverulenta*), mesquite (*Prosopis glandulosa*). Common shrubs

and small trees included Texas persimmon (*Diospyros texana*), huisache (*Acacia

minuata*), brasil (*Condalia hookeri*), lotebush (*Ziziphus obtusifolia*), colima

(*Zanthoxylum fagara*), la coma (*Sideroxylon celastrinum*), and granjeno (*Celtis pallida*),

often forming impenetrable thickets. Ground-level vegetation was primarily introduced

guinea grass (*Panicum maximum*), introduced buffel grass (*Pennisetum ciliare*), and

several herbaceous and semi-herbaceous broad-leaved species. Plant communities at the

study sites are further described by Vora (1990) and Lonard and Judd (2002). Plant

taxonomy follows Jones et al. (1997). Common names of plants follow Richardson (1995).

RECENT POPULATION TRENDS

I examined Audubon Christmas Bird Count (CBC) data from Anzalduas-Bentsen and Santa Ana. I calculated five-year averages of the number of Altamira Orioles seen per party-hour to reduce the variability, after Brush (1996).

NEST SEARCHING AND MONITORING

Nests were located either by following orioles that showed nesting behavior (Martin and Geupel 1993) or by random search during times of the day when oriole activity was low. Field assistants and I searched all sites except La Joya, Madero Residential, and Marinoff from mid-March until the end of August of both years. La Joya was only searched from mid-May until the end of July of both years because of logistical constraints. Marinoff and Madero Residential were searched by driving through the sites via automobile; Marinoff was searched during both years, and Madero Residential was searched only in 2003 (Table 1). I focused nest-searching and monitoring efforts on Bentsen and Santa Ana because of their large size and abundance of orioles during preliminary surveys. My field effort was slightly greater in 2003 because of one additional field assistant. I also collected data during 2002-2003 for a nesting study on Northern Beardless-Tyrannulets, so effort was split among the two projects. I canoed the entire stretch of the Rio Grande at Santa Ana once per season (25 May 2002 and 26 June 2003) to find nests along the river that likely would not have been found otherwise. I considered nests located just outside a site's boundaries as part of that site if the adults

spent a noticeable amount of time using habitat on the site.

I recorded locations and nest-tree species of all completely-built nests, even if they appeared inactive. A nesting attempt was defined as anytime an oriole laid at least one egg in a nest, even if the nest was reused after a previous clutch had been laid within the same nest. Most nests were monitored at least every 3 to 5 days, with more frequent visits during transition periods (e.g., hatching, fledging). I used standard procedures during nest visits to minimize human disturbance (Martin and Geupel 1993). At each nest, I recorded the age of the male and female in the breeding pair as subadult or adult. Altamira Orioles have mostly yellow, olive, and brown plumage until the second prebasic molt, after which they attain the characteristic bright orange and black plumage (Dickey and van Rossem 1938, Pyle 1997). I assumed that females did most or all of the nest-building and incubation (Brush 1998a). Nesting attempts were considered successful if a nest fledged at least one oriole, and failed if this did not occur. When I could not find fledglings near an empty nest, the nest was assumed to have fledged if, during the previous visit, the nestlings were 12 days old or begging very loudly and the nest was still intact during the final visit.

I made most nest observations from a distance using binoculars, and determination of the nesting stage was facilitated by using a nest-inspection camera (Proudfoot 1996, 2002) in nests that were accessible and below 11.2 m. Altamira Oriole eggs were distinguished from those of Bronzed Cowbirds and Brown-headed Cowbirds (*Molothrus ater*) by using descriptions and illustrations of Baicich and Harrison (1997). For nests that were inaccessible to the camera, the presence of cowbird nestlings was

determined by standing close to the nest and listening for cowbird begging calls. The begging calls of Bronzed Cowbird and Brown-headed Cowbird nestlings are much harsher and persistent than those of Altamira Oriole nestlings, especially in that cowbird nestlings continue to beg loudly long after the adult has left the nest to forage, whereas oriole nestlings generally do not (Hathcock 2000; S. M. Werner, personal observation).

Although none of the orioles were color-banded, I was able to keep track of multiple nesting attempts by the same female or breeding pair with a moderate level of certainty. This is because Altamira Orioles are solitary nesters and very few territorial interactions are seen during the nesting season (Pleasants 1977), and the presence of subadults in the breeding population that I studied allowed for a higher probability of identifying individuals than if all breeding birds had shown adult plumage. Furthermore, several Altamira Orioles at Bentsen displayed unusual plumage patterns (S. M. Werner, unpubl. data), allowing for a fairly confident identification. The assumption of solitary nesting allowed me to estimate yearly productivity. I defined a breeding pair as a pair of birds occupying a consistent territory, which was estimated as birds were followed in the habitat to and from their nests. "Breeding pairs" also included unseen females and males that built nests that were inactive when I found them, as long as I had no indication that the nest was built by a previously seen pair. I estimated the number of breeding pairs at each site, and inactive nests were generally assumed to be from the same pair if they were within 300 m of each other. Locations of nests were recorded using a handheld GPS device (Map 330M; Magellan Corporation, San Dimas, California, USA) and plotted on digital orthophoto quadrangles (DOQs) using ArcView 8.3 (ESRI 2002).

NESTING SUCCESS

Determining lengths of nest stages. I visited easily-accessible nests every 1-2 days to obtain accurate estimates of incubation, hatching, and fledging events. I made two assumptions for the final estimates: (1) Altamira Orioles lay 1 egg per day (Martin and Geupel 1993), and (2) they lay their eggs during the early morning within 2-3 hours of sunrise, like other icterids (Scott 1991). To calculate the incubation and nestling periods, I created a list of nests for which I knew the exact date of incubation, hatching, or fledging accurate to several hours. This exact list was then supplemented by a list of other nests for which I either knew the period accurate to 1 day, or knew the minimum period through distant observation. Final period lengths were estimated to the nearest half-day as Martin et al. (1997) suggest for calculating exposure days.

I compared the lengths of the nest-building period of early and late nests, where early and late were defined as having initiated building on or before 15 May, and after 16 May, respectively. This comparison did not include nests that were reused for a second clutch.

Nest survival. I calculated daily nest survival rates, standard errors, and survival probabilities according to Mayfield (1961, 1975) and Johnson (1979). I followed Mayfield's (1961, 1975) and Martin et al.'s (1997) suggestions for determining exposure days. I used the average incubation and nestling lengths to "back-compute" hatching events and the onset of incubation when my field observations were less accurate. For failed nests I calculated the fail date as the half-way point between the last confirmed active date and the date on which the nest was confirmed not active. I excluded nests for

which the stage at failure was unknown and could not be estimated.

Altamira Oriole productivity. I determined an average number of eggs laid for nests that I inspected within 5 days of the start of incubation to minimize partial predation effects. I compared the number of fledglings produced from early and late clutches, where early and late clutches were defined as having begun incubation before 1 June, and on or after June 1, respectively (the difference between early and late clutches, defined here, and nests, defined above, accounts for the long nest-building time). For numbers of fledglings produced by nests and breeding pairs, I excluded nests with uncertain outcomes.

COWBIRD VISITS TO ALTAMIRA ORIOLE NESTS

I determined the rate of nest visits and nest entries by Bronzed and Brown-headed Cowbirds into oriole nests by tallying all cowbird visits seen during all timed monitoring sessions. Because monitoring sessions were usually longer at nests that were inaccessible to the camera, these nests were more represented in the total sample. I defined a nest visit as any time a cowbird approached to within 2 m of a nest, whether perched or hovering, which is different from Hathcock (2000), who counted visits every time a cowbird either looked into or entered a nest. I wanted to determine cowbird visits regardless of whether the orioles chased them away (which is usually what occurred if a cowbird landed nearby a nest but did not get close enough to look inside or enter). For example, a single cowbird near the nest counted as one visit, and a flock of three cowbirds near the nest counted as three visits. I ignored the sex of the cowbirds because male and female Bronzed Cowbirds are sometimes difficult to tell apart in the field

depending on the lighting, the distance from the observer to the nest, and how quickly

the cowbird visit takes place. (Most cowbirds that approached nests were female.) I

present observations during all times (CST) of day as well as observations starting

between 0600 hrs and 1100 hrs to compare with Hathcock's (2000) results. I only

analyzed data from active nests, excluding nests that were abandoned during building,

because sometimes I was not sure if a nest had already been abandoned during the

monitoring session.

HABITAT MEASUREMENTS

At each oriole nest I took two groups of measurements, representing different scales: (1)

nest-placement variables that described local placement of the nest, and (2) nest-site

variables that described the vegetation around the nest at a larger scale than nest-

placement data.

Nest-placement variables. At nests I recorded tree species, nest tree height,

diameter at breast height (dbh) of the nest tree, nest height at nest opening, azimuth from

the nest-tree trunk to the nest ("trunk-to-nest angle"), compass direction of the nest-

opening ("nest-opening angle"), and horizontal distance from the nest-tree trunk to the

nest. Compass bearings were corrected for magnetic declination and recorded for true

north. Heights below approximately 8.5 m were measured with a telescopic pole, and

heights above 8.5 m were measured with a clinometer.

Nest-site variables. I measured vegetation at the nest site using a 0.04-ha circular

plot (James and Shugart 1970, Martin et al. 1997) centered at the nest. I used a paired,

random-plot design to identify features of the vegetation that were more likely to be

associated with oriole nests. The center of the 0.04-ha circular non-use plot was located at a random compass direction and a random distance between 20 and 50 m from each nest. I limited this distance to 50 m to avoid placing the non-use plot in a distinctly different habitat such as a grassland, wetland or the Rio Grande. Like nests, non-use plot locations were recorded with the GPS device. I measured the same nest-site variables at all nest plots and non-use plots. I recorded the number, dbh, and species of small trees (dbh 15-30 cm), large trees (dbh > 30 cm), and snags (dbh > 15 cm, height > 1.4 m), and the number of fallen logs (diameter > 15 cm and length > 3 m). Canopy cover was measured using a concave densiometer at the center of the plot.

Within each plot I placed four 10-m transects in the cardinal directions emanating from the center of the plot. At point intervals of 2 m along the transects I placed a 7.6-m telescopic pole and counted the number and species of vegetation hits (Wiens and Rotenberry 1981) in each 1-m vertical layer. Thus the total number of points sampled with the pole in the plot was 21 (five points per cardinal transect and one center point). Pinnately compound leaves were counted as one hit each. The maximum number of *Tillandsia* hits per 1-m layer was 10 for simplicity (hits of other species could exceed 10 per layer, but this rarely happened). Hits above 7.6 m were estimated after obtaining the nest and tree heights, usually with a clinometer. At each of the 21 points I measured the maximum canopy height within 10 cm of the pole, and the maximum of these heights was the maximum height variable for the plot.

I divided the vertical profile into three strata to describe the ground layer (0-1 m), shrub layer (1-3 m), and tree layer (>3 m). Pole hits were calculated into two primary

variables. Foliage frequency was defined as the sum of the points with foliage hits,

divided by the total number of points (21) on the plot. Foliage frequency was calculated

for the three vertical layers and also graphically represented for each 1-m layer. Foliage

density was defined as the number of foliage hits summed at all 21 points in each of the

three layers.

I used two indices of structural heterogeneity at the plot. I calculated the

variation in vegetation height across the plot using the heterogeneity index of Wiens and

Rotenberry (1981), where height variation = (maximum vegetation height – minimum

vegetation height)/mean vegetation height. A height-variation value of zero indicates a

uniform height across the plot, whereas a large value indicates more variation in the

height of the foliage on the plot. I calculated vertical structural diversity (VSD) among

the three vegetation layers using a Simpson diversity index (Hill 1973) following Braden

(1999): $VSD = 1/\Sigma(p_i^2)$, where p_i is the proportion of foliage hits in vertical layer i on a

plot. A VSD near 1 indicates large variation in hits among the three layers, while a VSD

of 3 indicates no variation in hits among the three layers.

Floristic composition of plots. To compare which plant species were most

commonly associated in the shrub and tree layers of nest plots and non-use plots, I

summarized the pole-hit data using importance values derived in a similar manner to that

of Lonard and Judd (2002). For each species I pooled hits from live and dead plant

material. The density of a species was the total number of foliage hits at all nest plots or

non-use plots. Frequency was defined as the proportion of plots at which a species was

present in that layer (tree or shrub). Relative frequency and relative density were

summed to give the importance value for the species in the shrub and tree layers.

Importance values thus describe how often a species occurs at plots and how much space

the species occupies at the plot. For simplicity I present only the species with the five

greatest importance values for each plot-type and layer. Importance values were

calculated for the three sites with the most nests: Bentsen, Santa Ana, and La Joya.

STATISTICAL ANALYSES

Nesting success. I used the program CONTRAST with a with a chi-square test to

compare daily nest survival rates between incubation and nestling stages, between sites

within nest stages, and between adult breeding pairs and breeding pairs with one or two

subadults within nest stages (Hines and Sauer 1989). I also compared the incubation and

nestling stage predation rates between this study and a previous study. I used a Kruskal-

Wallace test to compare oriole fecundity among study sites.

Cowbird visitation rates. I pooled my nest monitoring sessions during each

nesting stage during all times of the day for each nest and then compared the cowbird

visitation rates among years and stages with Mann-Whitney *U*-tests and Kruskal-

Wallace tests. I also compared cowbird visits per hour between nests that eventually

fledged and nests that eventually failed due to reasons other than from falling down, with

a Mann-Whitney *U*-test.

Nest-placement and nest-site selection. I calculated the mean angle, $\bar{a}$, of the

trunk-to-nest angle and nest-opening angle, and the average daily wind direction during

April, May, and June, 2002-2003 from the weather station at McAllen-Miller

International Airport (National Climatic Data Center 2003). I used Rayleigh's test (Zar

1996) to test the null hypothesis that each of these distributions was random. I compared

nonrandomly-distributed stem-to-nest angles with wind direction, and nonrandomly-

distributed stem-to-nest angles and nest-opening angles between successful and

depredated nests using a Watson-Williams test with an F ratio.

I used Matched-pairs Logistic Regression (MPLR) to explore habitat preferences

for nest placement (Hosmer and Lemeshow 2000). First, mean differences of nest-site

variables between nest plots and non-use plots were calculated. To select variables for

the multivariate MPLR, I entered each of the 14 nest-site variables into a univariate

MPLR and retained the variable if the Likelihood Ratio Test was significant at $P < 0.25$,

as recommended by Hosmer and Lemeshow (2000). I then checked for collinearity

among the selected variables. If a pair of variables was highly correlated ($|r| > 0.60$; $P <$

0.001), I entered each into separate multivariate analyses, ensuring that both were not

included in the same model, following Beck and George (2000) and Chase (2002). To

obtain reduced MPLR models I used a backward elimination method, starting with a full

model and eliminating variables when they did not significantly contribute to the model

(Likelihood Ratio Tests, $P < 0.10$). Following Hosmer and Lemeshow (2000), I checked

for linearity in the logit and checked for plausible interaction terms in the reduced

models. For the final models I assessed goodness of fit using the residual analyses

outlined by Hosmer and Lemeshow (2000), because current major statistical packages

lack a goodness of fit test for MPLR. I compared the final models using Akaike's

Information Criterion for small samples (AIC_c) as recommended by Burnham and

Anderson (2002). The best model of the group was the one with the smallest AIC_c. I

present only those models with AIC_c differences (Δ_i) less than 10.

Nesting-outcome habitat differences. I used binary logistic regression with a likelihood ratio statistic to compare mean habitat variables between successful and depredated nests. I chose variables for a multivariate binary logistic regression model in the same manner as with the MPLR for nest-site selection. "Nests" in this analysis were actually nesting attempts, 14 of which took place in only seven different reused nests. For these comparisons, I considered each nesting attempt an independent datum, assuming that the outcome for each reused nest was not dependent on the outcome of the other attempt (no nests were reused more than once). I measured vegetation once at each nest, so each pair of reused nests had the same habitat measurements.

I used SPSS for Windows, versions 11.0 and 12.0 (SPSS 2001, 2003) for all statistical analyses except Rayleigh's test and daily survival rate differences. An alpha level of 0.05 was used for all tests unless noted otherwise. Means are presented as ± 1 SE.

RESULTS

During 2002 and 2003 combined I located 89 fully-built oriole nests in approximately 55 territories in the study area (Table 3). There were two additional breeding pairs in 2002 on the Mexican side of the Rio Grande across from Santa Ana whose nests I couldn't locate. I found nests in these territories in 2003. Thirteen of the 89 nests were either inactive or unable to be checked regularly. Of the other 76 nests, seven were reused for a second clutch. Thus I monitored 83 total active nesting attempts (hereafter referred to in the nesting success context as 'nests' for simplicity).

Table 3. Distribution of monitored and unmonitored nests found ($n = 89$) and approximate number of associated nesting pairs of Altamira Oriole in the Lower Rio Grande Valley, Texas, 2002-2003. Area searched varied among sites and varied slightly between 2002 and 2003. No birds were color-banded to determine exact number of breeding pairs.

Site	2002 nests			2003 nests		
	monitored	not monitored	pairs	monitored	not monitored	pairs
Bentsen	17	1	10	18	1	11
El Morillo Banco	1	1	1	3	2	3
Gabrielson	0	0	0	3	0	1
La Joya	4	1	4	5	0	5
Madero tract	2	0	2	0	0	0
Madero residential	0	0	0	0	3	2
Marinoff	0	0	0	1	1	1
Santa Ana	8	0	5 [b]	14	3	10
Total	32	3	22	44	10	33

[a] Seven nests were reused for a second clutch so the total number of nesting attempts is $n = 96$.

[b] Two additional breeding pairs at Santa Ana in 2002 were nesting on the Mexican side of the Rio Grande (and used Santa Ana for foraging) and their nests were never seen.

The proportions of adults and subadults in the breeding population studied were remarkably similar during both years. Of the 53 breeding pairs that I identified at the nests, 82% of the 2002 birds were adults, and 81% of the 2003 birds were adults. The 2002-2003 female adult-to-subadult ratio was 3.4:1, and the 2002-2003 male adult-to-subadult ratio was 5.6:1. Approximately 72% ($n = 38$) of the breeding pairs were adult-adult pairs. Six percent ($n = 3$) were adult females paired with subadult males, 13% ($n = 7$) were subadult females paired with adult males, and 9% ($n = 5$) were subadult females paired with subadult males. Most subadult nests were found at Bentsen (Table 4).

RECENT HISTORICAL TRENDS AT THE STUDY SITES

The number of Altamira Orioles detected on Christmas Bird Counts at Santa Ana and the Bentsen-Anzalduas area peaked in the early 1970s after a steady rise beginning in the early 1950s (Figure 2). These oriole populations appeared to decrease substantially thereafter during the 1980s, followed by a rise and subsequent slight decrease in recent years.

NEST DISTRIBUTIONS AT THE SITES

Bentsen-Rio Grande Valley State Park had the highest numbers of breeding pairs and nesting attempts per site during both years (Table 3), which suggests that this park supported the highest densities of breeding Altamira Orioles anywhere in the LRGV, given its small size. The 2003 density of breeding pairs at Bentsen was 1 pair per 21.6 ha (calculated from the raw area of the park, although some oriole territories extended outside park boundaries) compared with an estimate of 1 pair per 85.3 ha at Santa Ana. El Morillo Banco tract, adjacent to Bentsen, supported several pairs in the riparian strip

Table 4. Number of successful (+) and failed (-) Altamira Oriole nesting attempts (n = 80) grouped by known age composition of breeding pairs at sites in the Lower Rio Grande Valley, Texas, 2002-2003.

breeding pair age type			Site[a]						
female	male	outcome	B	SA	LJ	EMB	G	MD	MR
adult	adult	+	20	10	5	2	2	1	1
		-	10	9	0	2	1	1	0
adult	subadult	+	3	0	0	0	0	0	0
		-	2	0	0	0	0	0	0
subadult	adult	+	3	0	1	0	0	0	0
		-	1	0	1	0	0	0	0
subadult	subadult	+	0	0	1	0	0	0	0
		-	0	2	1	1	0	0	0

[a] Site codes: B = Bentsen;, SA = Santa Ana; LJ = La Joya; EMB = El Morillo Banco; G = Gabrielson; MD = Madero; MR = Marinoff.
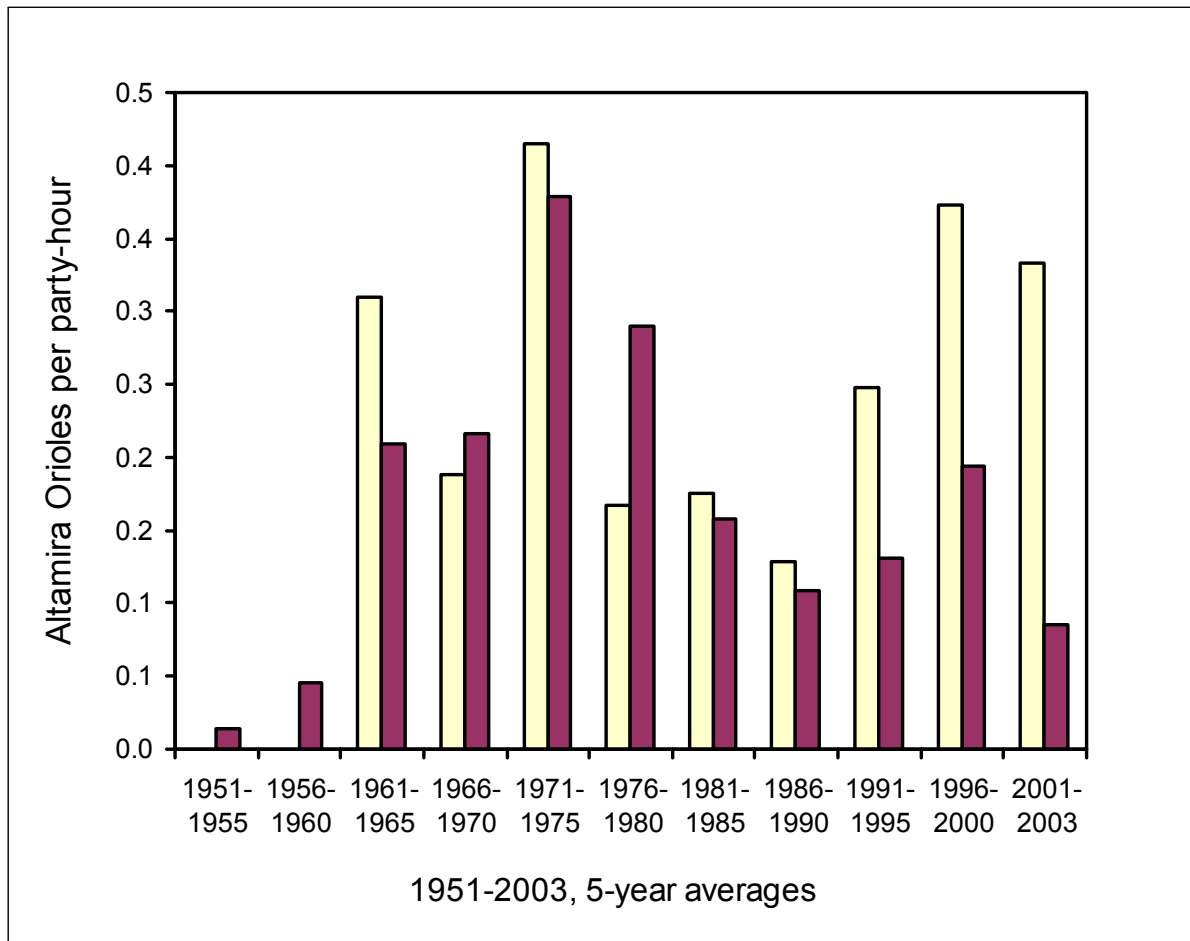
Figure 2. Trends in five-year averages of the number Altamira Orioles detected on Audubon Christmas Bird Counts (CBC) in two count circles in the Lower Rio Grande Valley, Texas. Shaded bars represent the Santa Ana CBC, and light bars represent the Anzalduas-Bentsen CBC.

along its large resaca (which was dry during this study). Trends from the CBC, along

with my data, suggest that the Altamira Oriole population at Bentsen was at its highest

level since the 1970s.

Most areas at Bentsen with tall cedar elms, sugar hackberries, or Mexican ashes

had an associated oriole pair. At Bentsen, oriole nests were not found in areas of thorn

scrub dominated by mesquite, such as around most of the Singing Chaparral Trail, the

central area, and the area circumscribed by the Rio Grande Hiking Trail (Figure 3). The

distribution of oriole nests at El Morillo Banco primarily followed the edge of the large

resaca, which was dry during 2002-2003 (Figure 3).

At Santa Ana, many nests were found in the northern wetland area around

Willow Lakes and Pintail Lakes. Here, nests were built in large trees emergent over the

surrounding scrub or in trees arranged linearly along the ponds. Nests elsewhere on

Santa Ana were generally located in scattered elm-hackberry woodland and thorn forest,

or in large trees along the Rio Grande (Figure 4).

Nests at Gabrielson and Madero were located in cedar elm or sugar hackberry in

scattered thorn forest (Figure 5). During both years I was unable to search most of the

southern wetland area of Madero, which could be excellent nesting habitat due to the

large trees at the water's edge, as seen from a distance and in aerial photos. At La Joya,

most of the nests were found along a riparian strip in the southeastern portion of the

tract. I did not search the riparian strip in the southwestern portion of the tract (Figure

5). However, two nests in 2002 were located in the upland area in separate tepeguajes.

This and most of the upland portions of La Joya have been reclaimed from agricultural
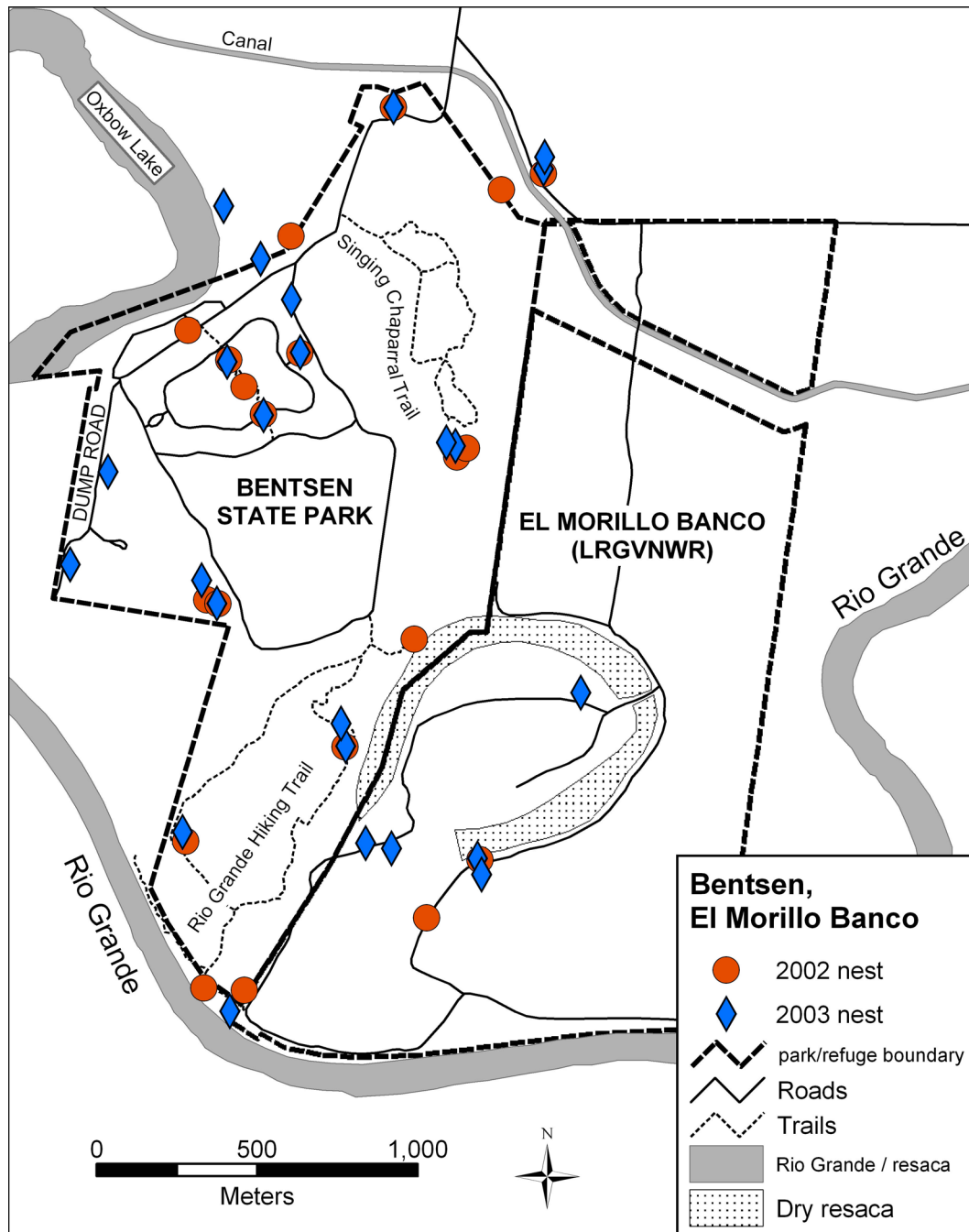
Figure 3. Locations of Altamira Oriole nests at Bentsen-Rio Grande Valley State Park and El Morillo Banco tract of the Lower Rio Grande National Wildlife Refuge, 2002-2003.
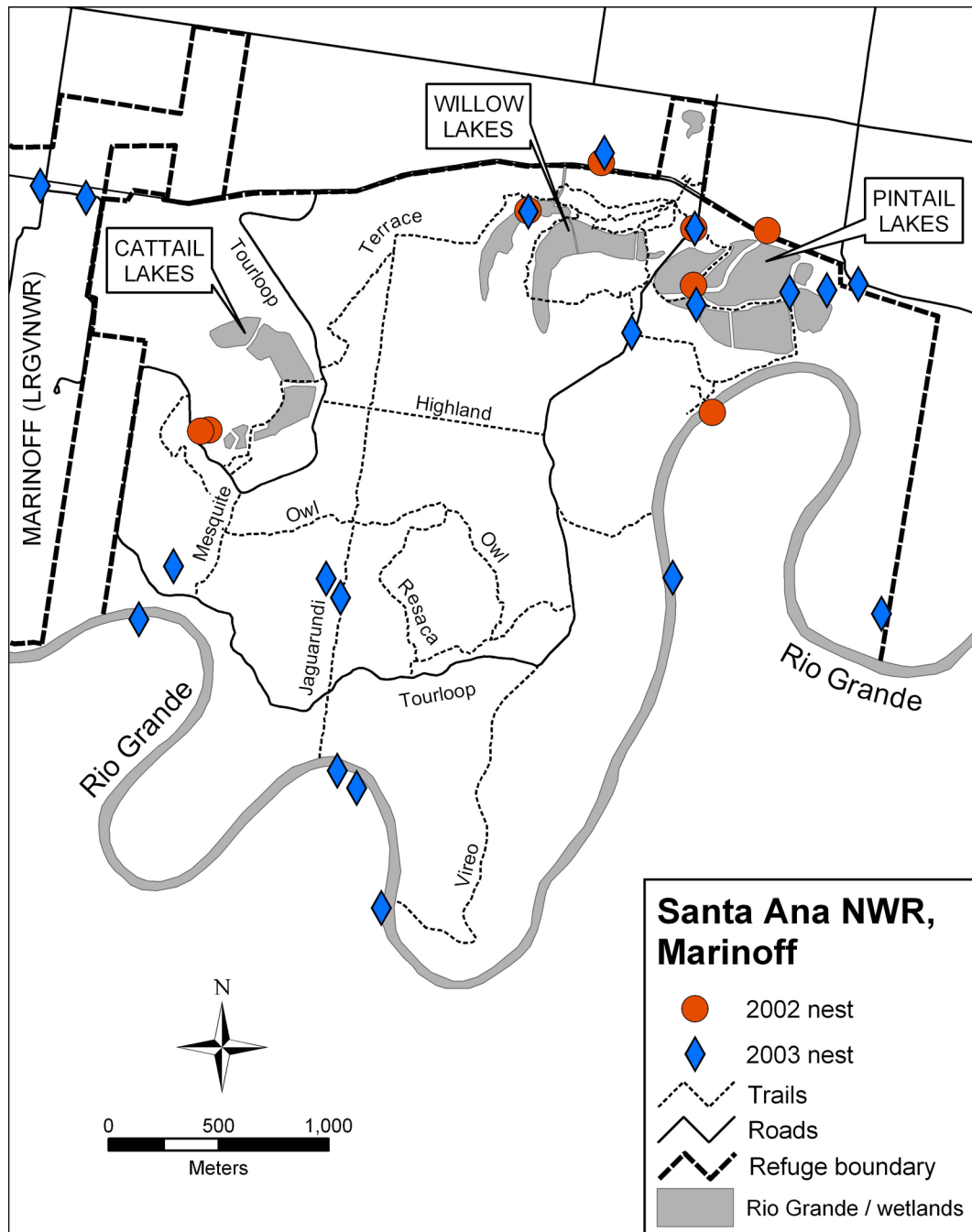
Figure 4. Locations of Altamira Oriole nests at Santa Ana National Wildlife Refuge and Marinoff tract of the Lower Rio Grande National Wildlife Refuge, 2002-2003. Map does not include two suspected nests on the Mexican side of the Rio Grande during 2002 at the southern ends of Jaguarundi and Vireo trails.
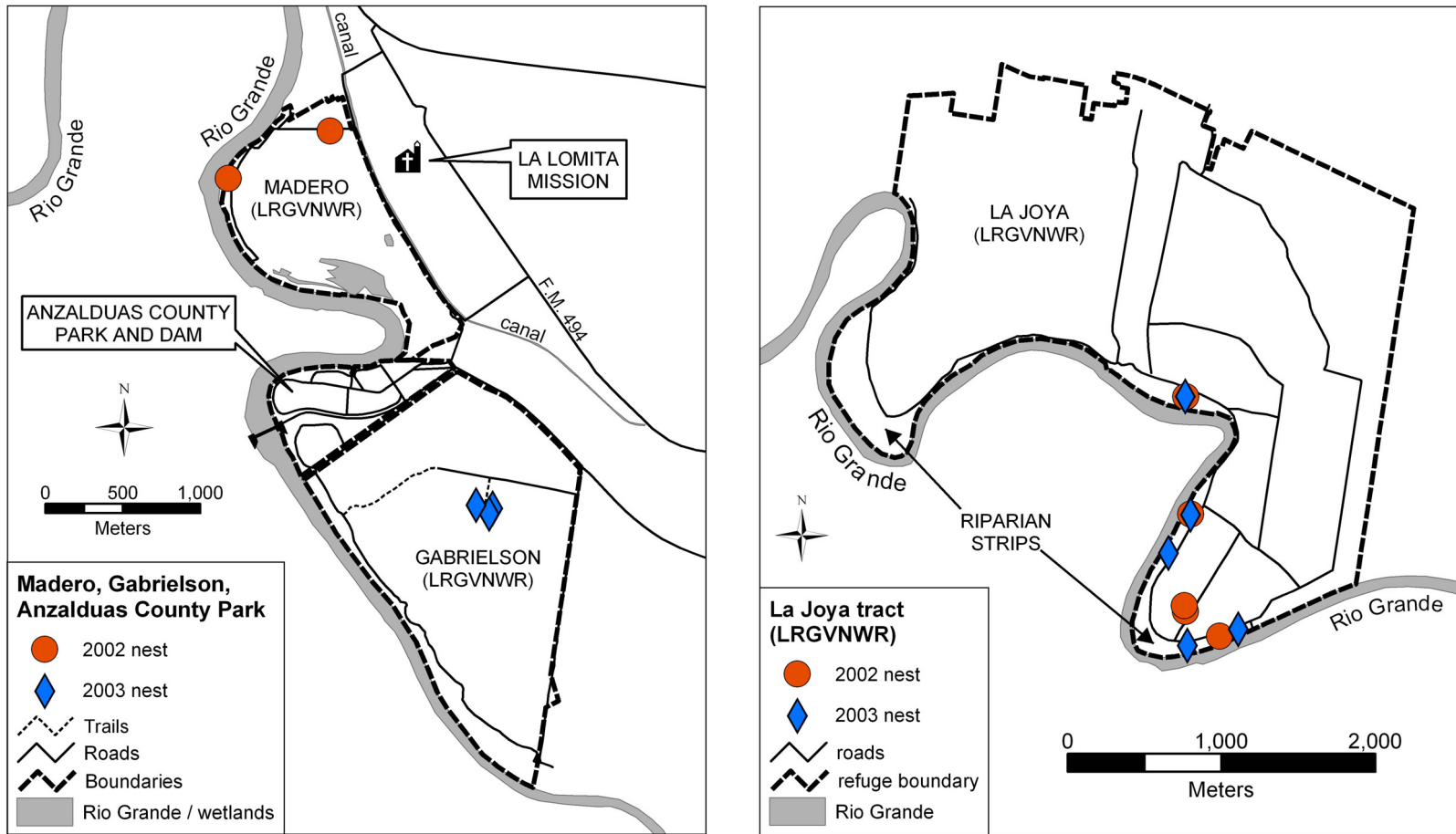
Figure 5. Locations of Altamira Oriole nests at the Madero, Gabrielson, and La Joya tracts of the Lower Rio Grande Valley National Wildlife Refuge, Texas, 2002-2003. Riparian strips at La Joya were delineated by the river and the adjacent levee road, shown as a solid line.

fields and replanted with huisache, tepeguaje, and other native plants.

NESTING PHENOLOGY

The first dates of nest-building during each year were 7 April 2002 and 28 March 2003.

The latest, completed nest of either year was begun on 2 July 2002. Early nests took 20

± 1.6 days (n =18; range 9-31) to build, and late nests took 11 ± 1.2 days (n =10; range

7-19) to build. The first oriole eggs of each year were laid on 30 April 2002 and 20

April 2003, and the last active dates of each year were 13 August 2002 and 7 August

2003, which were both dates of fledging events.

I knew the exact date of either incubation, hatching, fledging, or combinations of

the three events, for 14 nests. The means of the exact stage lengths were as follows:

incubation 12.5 ± 0.3 days (n =10; range 11-14); nestling 15.2 ± 0.3 days (n =7, range

14-16); incubation plus nestling 28.1 ± 0.6 days (n =8; range 26-31). Final lengths after

considering the rest of the nest data, rounded to the nearest half-day, were 12.5 days for

incubation, 15.5 days for nestling, and 28.0 days for incubation plus nestling.

NESTING SUCCESS

Of 83 oriole nesting attempts, 49 (59%) were successful and 31 (37%) failed. One nest's

outcome was unknown, and two nests likely fledged one or more young (they were

active late into the nestling stage), but I was uncertain whether the young were cowbirds

or orioles. Of the 31 failed nests, seven (23%) failed during egg-laying, 17 (55%) failed

during incubation, and 4 (13%) failed during the nestling stage. I was uncertain about

the stage at failure of the remaining three failed nests, and these nests were not

accessible with the camera. Six oriole nests fledged Bronzed Cowbirds, but two of these

nests also produced oriole fledglings.

I excluded six nests from the Mayfield analysis, because three nests had uncertain outcomes and three nests failed during an unknown stage (two of these nests fledged Bronzed Cowbirds and were inaccessible to the camera). There was no difference in daily nest survival during incubation between 2002 and 2003 (Table 5), but 2002 nests had a greater daily survival rate during the nestling stage than 2003 nests (χ^2_1 = 5.1, P = 0.02; Table 5). However, I pooled data from both years for all other survival rates because of small yearly sample sizes, following Hensler and Nichols (1981). Nests had a higher daily survival rate during the nestling stage than during the incubation stage (χ^2_1 = 8.0, P < 0.01). Because of this difference, I analyzed the incubation and nestling stages separately for between-site comparisons and adult vs. subadult comparisons, even though n < 20 for some categories. There was no difference in the daily survival rate between sites for either nest stage (incubation: χ^2_1 = 0.9, P = 0.6; nestling: χ^2_1 = 4.2, P = 0.12). Subadult nests appeared to have a greater daily survival than adult nests (χ^2_1 = 4.0, P < 0.046).

ALTAMIRA ORIOLE PRODUCTIVITY

For the 30 nests that I inspected within the first 5 days of incubation, the clutch size was 3.9 ± 0.2 (range 2-6) eggs. Early nests (n = 19) had 4.2 ± 0.2 eggs and late nests (n = 11) had 3.5 ± 0.3 eggs. Because my ability to identify the number of nestlings with the camera was limited, I knew the exact number of fledglings for only 14 of the 49 successful nests. For many of the other 35 nests I probably located all of the fledglings but I could not be certain. The mean number of fledglings per successful nest was 2.3 ±

Table 5. Mayfield daily survival rates for Altamira Oriole nests during the incubation (INC), nestling (NSTL), and incubation and nestling (I+N) stages in the Lower Rio Grande Valley, Texas, 2002-2003. Daily nest survival values of grouped rows were compared with the program CONTRAST. Asterisks indicate significantly different survival rates (*$P < 0.05$, **$P < 0.01$).

Nest stage / group	Daily nest survival	SE	Nest success (%)[a]	n	Exposure days
All 2002 nests INC	0.975	0.009	73.0	28	281.5
All 2003 nests INC	0.976	0.007	74.3	39	425.0
All 2002 nests NSTL	1.000*	0.000	100.0	22	337.0
All 2003 nests NSTL	0.991*	0.004	87.0	31	448.0
All nests INC	0.976**	0.006	73.8	67	706.5
All nests NSTL	0.995**	0.003	92.4	53	785.0
All nests I+N	0.986	0.003	67.2	70	1491.5
Bentsen INC	0.979	0.008	77.2	34	341.0
Santa Ana INC	0.980	0.010	77.8	17	201.0
Other INC	0.964	0.015	62.8	16	164.5
Bentsen NSTL	0.998	0.002	96.3	27	408.0
Santa Ana NSTL	0.984	0.009	77.8	13	186.5
Other NSTL	1.000	0.000	100.0	13	190.5
Adult pairs[b] INC	0.982	0.006	79.4	52	547.0
Subadult pairs[c] INC	0.956	0.016	57.1	15	159.5
Adult pairs NSTL	0.994*	0.003	91.0	45	660.0
Subadult pairs NSTL	1.000*	0.000	100.0	8	125.0

[a] Overall survival was calculated as (Daily nest survival)$^{12.5}$ for INC, (Daily nest survival)$^{15.5}$ for NSTL, and (Daily nest survival)^{28} for I+N.

[b] Breeding pairs in which each bird had full adult plumage

[c] Breeding pairs in which either the male or the female, or both, had subadult plumage

0.2 ($n = 49$; range 1-5). Nests with adult parents produced 2.4 ± 0.2 fledglings ($n = 41$) and nests with one or two subadults as parents produced 1.6 ± 0.3 fledglings ($n = 8$).

For the 47 breeding pairs that had 80 nesting attempts with known outcomes, the mean number of orioles fledged per nest was 1.4 ± 0.2. There was no difference in the number of orioles fledged per nest among sites (Bentsen 1.5 ± 0.2, $n = 39$; Santa Ana 1.1 ± 0.3, $n = 21$; La Joya 1.7 ± 0.6, $n = 9$; other sites 1.3 ± 0.4, $n = 11$; Kruskal-Wallace $\chi^2_3 = 2.0$, $P = 0.6$). For yearly output per breeding pair, there was a trend toward higher fecundity at Bentsen (2.8 ± 0.4, $n = 21$) versus the other sites (Santa Ana 2.3 ± 0.7, $n = 10$; La Joya 1.7 ± 0.6, $n = 9$; other sites 2.0 ± 0.9, $n = 7$) but this difference was not statistically significant (Kruskal Wallace $\chi^2_3 = 2.8$, $P = 0.4$).

Multiple broods. The maximum number of successful broods by a single pair during a season was two. Twelve nesting pairs each fledged two broods during this study. All but 1 of these pairs were composed of two adults. The exception was a pair in which an adult female was mated with a male subadult. Six of these 12 pairs had an intermediate failed attempt between the first and second successful attempts. The maximum number of clutches laid by a single pair was four ($n = 1$). The mean time interval from a nest failure to laying the first egg in a newly built (i.e., not reused) nest was 12.1 ± 0.9 days ($n = 14$, range 7-18). The time interval from successfully fledging a brood to laying the first egg in a newly built nest was 19.6 ± 1.7 days ($n = 9$, range 15-29). I often saw females building new nests while their mates tended to recent fledglings nearby.

Reused nests. Seven nests were reused by apparently the same breeding pair that had originally used them. All females and males attending these nests were adults. Five of the nests were reused after having previously fledged orioles. The interval from fledging to re-laying for these five nests was 13.8 ± 3.7 days (range 6-27), and to my knowledge none of these five females attempted to rebuild a nest before occupying the original again. The sixth nest was reused after the two eggs in the original clutch failed to hatch. The seventh reused nest had originally failed early in the nestling stage, after which the female built two nests that failed during the incubation stage and the laying stage, in chronological order. The original nest was then re-occupied and fledged one or two fledglings. This nest was on a power line and inaccessible to the camera.

FACTORS AFFECTING NESTING SUCCESS AND PRODUCTIVITY

Three of the 31 nest failures were caused by the nest falling from the nest tree. Two nests fell when the nest branch broke (during incubation), and the third nest fell when the entire tree fell down during the nestling stage. This third nest contained four nestlings that likely would have fledged in 1 or 2 days, but given the enclosed structure of the nest, none survived after the fall. None of these three failure events appeared to be associated with any extreme weather events such as thunderstorms or tropical storms, although gusty afternoon winds were common at the study sites.

None of the 28 nests that failed from reasons other than falling appeared to have any structural damage (e.g., ripped open). I observed no predators enter any nests, but I observed 11 nest-entries by Bronzed Cowbirds, which are known to pierce host eggs and other cowbird eggs (Carter 1984). Only five of these entries were into nests containing

eggs, and I could not confirm if the cowbirds pierced any of the eggs. I documented 17 partial oriole clutch losses (i.e., when ≥ 1 egg had disappeared, ≥ 1 egg remained, and the nest remained active) from 12 different nests, which could have resulted from a Bronzed Cowbird piercing an oriole egg and then an oriole removing the egg. Only 1 Bronzed Cowbird egg was present during these inspections. Two nests that had experienced egg reduction subsequently contained only one and two eggs, respectively, and were eventually abandoned because the eggs never hatched even though they had been incubated. A different nest was abandoned after one of its two eggs disappeared. Since I did not know the starting date of incubation for this nest, it was not clear whether the egg failed to hatch after full incubation or was abandoned before its expected hatch date.

I observed no Brown-headed Cowbird eggs in any oriole nests. I observed Bronzed Cowbird eggs in six different nests, three of which remained active and two of which had been abandoned the day before. I also found 1 Bronzed Cowbird egg in an inactive nest that had been empty 4 days earlier. (Nests were not regularly inspected when they were no longer being used.) Of 15 broken oriole eggs observed in nests throughout the course of the study, only 1 egg conclusively appeared to have been pierced by a bird's bill.

I did not observe orioles removing any eggs from a nest, although I inspected two nests from which Bronzed Cowbirds eggs had been removed since my last visit. Of these, 1 nest contained 1 oriole egg and 1 Bronzed Cowbird egg at 1220 hr, and the following morning at 0754 hr the nest contained a single oriole egg. A different nest

contained three oriole eggs and four Bronzed Cowbird eggs at 0705 hr during the laying stage, and 2 days later at 1005 hr the nest contained five oriole eggs.

Six oriole nests were successfully parasitized by Bronzed Cowbirds: three at Bentsen, two at Santa Ana, and one at La Joya (Table 6). A seventh nest at Santa Ana was suspected to have fledged a cowbird because the nestling stage only lasted 11 to 13 days (too brief for an oriole) and this nest had been visited frequently by Bronzed Cowbirds. Two nests that fledged Bronzed Cowbirds also fledged orioles. Two (33%) of the six successfully parasitized nests had a subadult as part of the breeding pair (Table 6), which was similar to the proportion of subadult pairs (28%) in the sample population. One of the successfully parasitized nesting attempts occurred in a reused nest, after having fledged successfully the first time.

COWBIRD VISITS TO ORIOLE NESTS

Of 148 total cowbird nest-visits, 145 were made by Bronzed Cowbirds, and only three were made by Brown-headed Cowbirds. I performed the analysis with the Bronzed Cowbird data only. There were no differences in visitation rates for each nesting stage between 2002 and 2003. After pooling data from both years there were no significant differences of visitation rates among nesting stages whether observations were made during the morning hours ($\chi^2_3 = 5.78$, $P = 0.12$) or during all daylight hours ($\chi^2_3 = 5.38$, $P = 0.15$; Table 7). Five of the 11 nest entries by Bronzed Cowbirds were in nests still under construction, before laying occurred. The other nest entries were as follows: 1 during laying, four during incubation, and 1 during nestling. Bronzed Cowbird visitation

Table 6. Successfully parasitized Altamira Oriole nests by Bronzed Cowbirds in the Lower Rio Grande Valley, Texas, USA, 2002-2003. For age, F = female, M = male, A = adult, S = subadult.

Nest	*n* BROC fledged	*n* ALOR fledged	Site	Age F	Age M
2002BEN13[a]	2	2	Bentsen	A	A
2002LAJ04[c]	1 or 2	1	La Joya	S	S
2002SAN04	1	0	Santa Ana	A	A
2003BEN01-2	3	0	Bentsen	A	A
2003BEN10	3	0	Bentsen	A	A
2003SAN14	3	0	Santa Ana	S	S
2002SAN05[c]	1	0	Santa Ana	S	A

[a] Time interval between cowbird fledging and oriole fledging was 6 days
[b] Time interval between cowbird fledging and oriole fledging was 7 to 9 days
[c] This nest was suspected to have fledged ≥1 Bronzed Cowbird but was inaccessible to the camera and no cowbird fledgling was found.

Table 7. Comparison of Bronzed Cowbird visitation rates at Altamira Oriole nests (n) and total observation time among nest stages and between this study and Hathcock's (2000) 1997-1999 data in the Lower Rio Grande Valley, Texas. Time of day is Central Standard Time.

Time of day	Year of study	Stage	Visits hr^{-1}	SE	n	total obs. time (hr)
07:00-19:30	2002-2003[a]	BLDG	0.57	0.18	64	80.6
		LAY	0.84	0.38	44	21.9
		INC	0.55	0.13	68	97.2
		NSTL	0.16	0.05	57	128.6
07:00-12:00	2002-2003[a]	BLDG	0.66	0.22	54	57.2
		LAY	1.60	0.67	24	12.3
		INC	0.73	0.19	55	62.2
		NSTL	0.27	0.09	55	82.7
	1997-1999[b]	Pre-LAY	3.13	1.70	2	1.7
		LAY	2.81	0.78	8	7.5
		INC	0.57	0.19	20	50.2
		NSTL	0.60	0.19	15	30.6

[a] There were no significant differences of visitation rates among nest stages with observations from throughout the day (Kruskal-Wallace test, $X_3^2 = 5.38$, $P = 0.15$), and with observations during 07:00-1200 (KW $X_3^2 = 5.78$, $P = 0.12$).

[b] From Hathcock (2000), who found a significantly higher visitation rate during the laying stage than during the incubation and nestling stages. Hathcock's BLDG stage was actually the "pre-laying" stage, defined as "from closure of all sides of the nest during building to the laying of the first egg (Hathcock 2000:15)," whereas BLDG in this study was from the beginning of nest construction until the laying of the first egg.

rates did not differ significantly between successful and failed nests within stages (building: $U = 287$, $P = 0.6$; laying: $U = 139.5$, $P = 0.08$; incubation: $U = 451.5$, $P = 0.5$; nestling: $U = 120$, $P = 0.09$), but when all stages were pooled, successful nests had significantly fewer cowbird visits per hour than failed nests (successful: 0.35 ± 0.07 visits hr^{-1}, failed: 1.21 ± 0.55 visits hr^{-1}, $U = 455$, $P = 0.03$).

NEST-SITE SELECTION

Nest placement. Altamira Orioles built their nests in 12 different tree species, on low-voltage power lines, and on a television antenna on top of a house (Figure 6). In 2003, 11 nests were located within 5 m of a nest that had existed during 2002. Seven of these nests were apparently on the same limb, nearly exactly where a 2002 nest had been built.

Mean nest height was 8.8 ± 0.3 m (range 4.1-14.0, $n = 67$), mean nest tree height was 12.7 ± 0.3 m (range 7.7-18.4, $n = 63$), mean nest-tree dbh was 32.0 ± 1.1 cm (range 8.8-55.6, $n = 63$), and horizontal trunk-to-nest distance was 5.4 ± 0.2 m (range 2.3-10.5, $n = 63$). Trunk-to-nest angle was a nonrandom 316.5 degrees (Rayleigh's $z = 39.8$, $P < 0.001$, $n = 63$). Nest-opening angle was also nonrandom, at 311.7 degrees (Rayleigh's $z = 33.4$, $P < 0.001$, $n = 67$). The mean daily wind direction was nonrandom at 134.3 degrees (Rayleigh's $z = 116.6$, $P < 0.001$, $n = 162$). The nest-to-trunk angle of 136.5 degrees (the opposite of 316.5 degrees) was not significantly different than the mean wind direction (Watson-Williams $F_{1,223} = 0.18$; $P > 0.25$).

Nest-site selection. Nest plots had a lower foliage frequency than non-use plots at heights below 8 m, but nests plots generally had taller vegetation than non-use plots (Figure 7). Of the 14 nest-site variables considered for the nest-site selection MPLR, 10
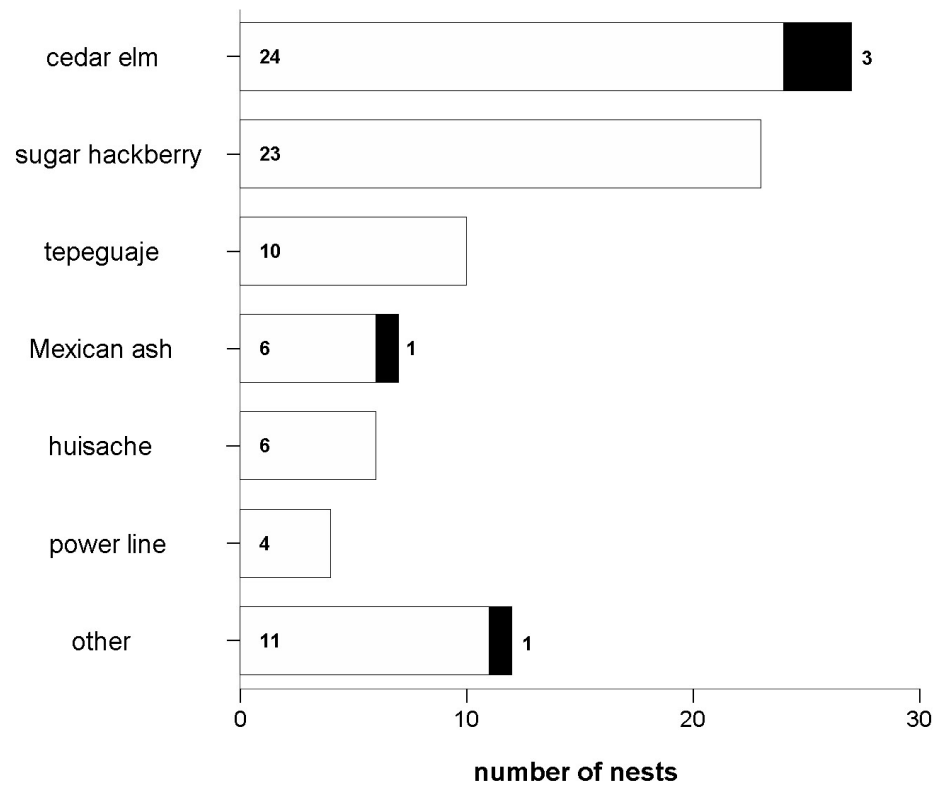
Figure 6. Distribution of nesting substrates for Altamira Orioles nests (*n* = 89) in the Lower Rio Grande Valley, Texas, 2002-2003. White sections of the bars represent live trees, and black sections represent dead trees. Other substrates were: bald cypress (*Taxodium mucronatum*; *n* = 2), black willow (*Salix niger*; *n* = 2), television antenna on a house roof (*n* = 2), Wright acacia (*n* = 2), retama (*Parkinsonia aculeata*; *n* = 1), dead mesquite (*n* = 1), tamarisk (*Tamarix* sp.; *n* = 1), and an unidentified ornamental species (*n* = 1). See text for other scientific names.

were significant at the $P = 0.25$ level in univariate analyses (Table 8). There was some collinearity among the significant variables. Canopy cover was excluded from models containing height variation (Spearman $r_s = -0.61$, $P < 0.001$), and tree-layer foliage density ($r_s = 0.73$, $P < 0.001$). Height variation and tree-layer foliage density were correlated ($r_s = -0.62$, $P < 0.001$) and shrub foliage frequency and shrub foliage density were correlated ($r_s = 0.82$, $P < 0.001$) and thus not included in the same multivariate MPLR models.

The best final MPLR model (Model 1) indicated that canopy cover, number of logs, and maximum height were the best predictors of nest-site selection (Table 9). Based on the Akaike weights, Model 1 had about three times the predictive power of the next best model ($w_1 = 0.574$ vs. $w_2 = 0.185$), which included number of logs instead of number of large trees. Canopy cover or maximum height, or both, were in all of the five best models. There were no significant plausible interaction terms in any of the models. I was satisfied by the fit of all five models after the residual analysis. Only three of the 63 nests appeared to be outliers, but I decided to leave the full dataset in the final models. These three nests differed from the rest of the dataset primarily in that they had lower maximum vegetation heights and fewer large trees their paired non-use plots. Given the heterogeneity of the habitat at these sites, and the fact that the oriole has been called a generalist in its nesting habits, my paired-plot design would be expected to produce a few atypical habitat differences.

Floristic composition of plots. Cedar elm, sugar hackberry, and huisache were the three most important species in the tree layers at Bentsen and Santa Ana (Table 10,
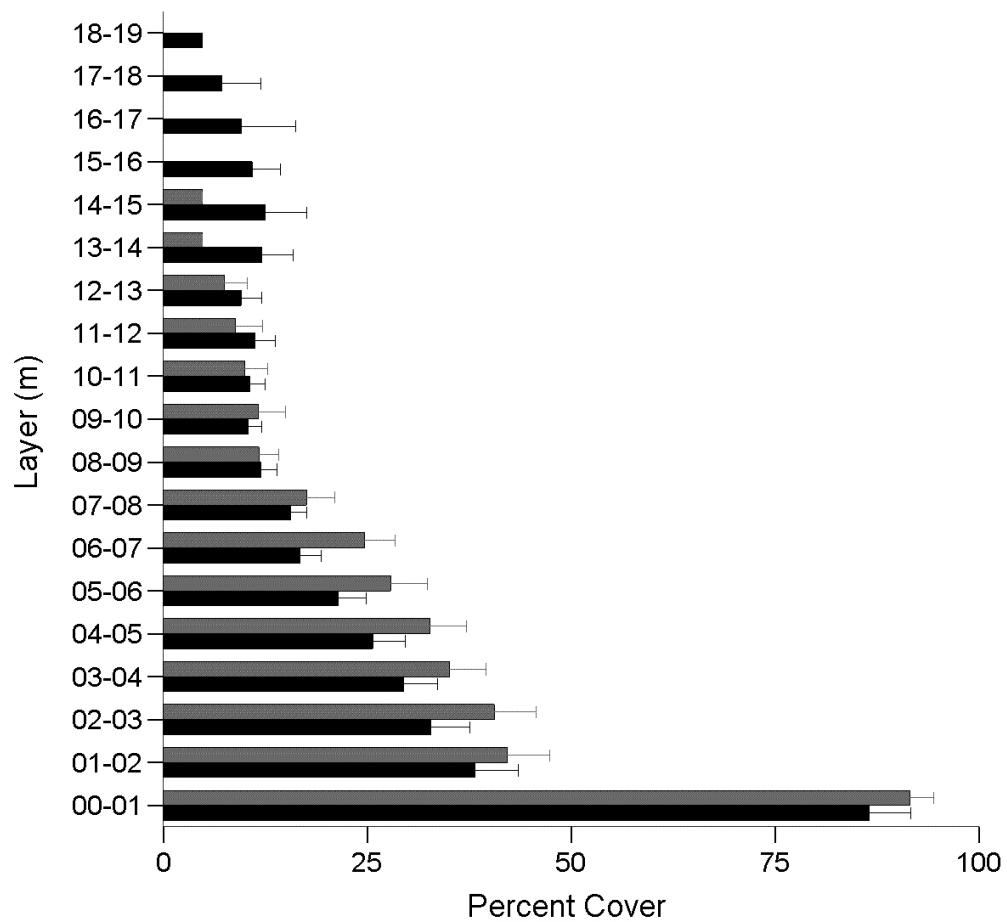
Figure 7. Foliage frequency for each vertical meter layer obtained from vegetation hits on a vertical pole placed at 21 points within nest plots (black bars; *n* = 66) and non-use plots (gray bars; *n* = 63) of Altamira Oriole nests in the Lower Rio Grande Valley, Texas, 2002-2003. Error bars represent 2 SE.

Table 8. Summary of mean differences of nest-site variables between paired nest plots and non-use plots for Altamira Oriole nests ($n = 63$) in the Lower Rio Grande Valley, Texas, USA, 2002-2003. Likelihood Ratio Test statistic (LRS χ^2_1) and P values are from univariate 1-1 matched pairs logistic regression (MPLR). Asterisks denote significance for inclusion in the multivariate MPLR ($P < 0.25$).

Variable	$\bar{x}$ difference	SE	LRS χ^2_1	P	Correlations[a]
% canopy cover	-6.0	4.5	1.8	0.19*	AB
Large trees (15-30 cm dbh)	0.3	0.4	0.4	0.51	
Small trees (>30 cm dbh)	0.4	0.2	5.6	0.02*	
Snags	0.5	0.3	3.2	0.07*	
Logs	1.9	0.5	16.2	<0.001*	
Maximum height	3.3	0.4	44.3	<0.001*	
Height variation	0.3	0.2	1.9	0.17*	AC
Foliage frequency, 0-1m (%)	-3.5	2.6	1.8	0.18*	
Foliage frequency, 1-3m (%)	-7.3	3.8	3.7	0.05*	D
Foliage frequency, >3m (%)	1.4	3.6	0.1	0.7	
Foliage density, 0-1m	-2.9	6.2	0.2	0.6	
Foliage density, 1-3m	-15.0	8.0	3.5	0.06*	D
Foliage density, >3m	-16.6	7.5	4.8	0.03*	BC
Vert. structural div. (VSD)	-0.1	0.1	1.2	0.28	

[a] Matching letters indicate variables that were significantly correlated (Spearman Rank Correlation; $|r_s| \geq 0.60$, $P < 0.001$) and thus were not included in the same multivariate model.

Table 9. Final MPLR models describing nest-site selection for Altamira Oriole nests (n = 63) in the Lower Rio Grande Valley, Texas, 2002-2003. LRS = Likelihood Ratio χ^2 Statistic; K = number of parameters; AIC_c = Akaike Information Criterion, Δ_i = AIC differences; w_i = Akaike weights.

Model # and variables	Coefficient	SE	LRS[ab]	K	AIC_c	Δ_i	w_i
1			62.6***	4	33.4	0.0	0.574
canopy cover	-0.065	0.023	16.1***				
# of logs	0.569	0.278	5.6**				
max. height	0.921	0.264	42.3***				
2			60.4***	4	35.7	2.3	0.185
canopy cover	-0.062	0.022	15.1***				
# of large trees	0.713	0.383	3.4*				
max. height	0.947	0.259	51.4***				
3			57.0***	3	36.7	3.3	0.108
canopy cover	-0.049	0.018	43.0***				
max. height	0.885	0.236	85.6***				
4			58.7***	4	37.4	4.0	0.079
logs	0.408	0.267	3.0*				
max. height	0.783	0.229	37.1***				
foliage density, >3 m	-0.027	0.010	12.1***				
5			55.6***	3	38.1	4.7	0.054
max. height	0.802	0.215	50.9***				
foliage density, >3 m	-0.024	0.009	11.3***				

[a] The LRS of the full model vs. null model is shown on the first row for each model, and the LRS for the full model versus the model without the variable is shown next to each variable.

[b] *P < 0.01; **P < 0.05; ***P < 0.001

Table 11). Granjeno was prevalent in the shrub layer of both plot-types at Bentsen and Santa Ana, but at La Joya it was absent from the top five shrub-layer species at nest plots (Table 12). Nests at Bentsen were primarily composed of cedar elm and sugar hackberry in the tree layer, while mesquite had a much higher importance value on non-use plots. The shrub layers of non-use plots at Santa Ana and La Joya seemed to have more vine species, such as serjania (*Serjania brachycarpa*) and snail seed (*Cocculus diversifolius*), than on the nest plots at those sites.

HABITAT DIFFERENCES BETWEEN SUCCESSFUL AND DEPREDATED NESTS

Nest-placement variables and nest-site variables were similar at successful nests and depredated nests (Table 13). Logs and shrub-layer foliage density were different in univariate analyses, but these two variables did not significantly contribute to a multivariate model. Successful nests had roughly twice as many logs and 58% greater foliage density in the shrub layer than depredated nests. Interestingly, shrub-layer foliage density at successful nests (81.5 ± 10.0; $n = 46$) approached the value of shrub-layer foliage density in the available habitat, or non-use plots (85.3 ± 6.5; $n = 63$).

Of the commonly-used nesting species or substrates, none appeared more likely to result in a failed or successful attempt (Figure 8), but all nests built in huisache and retama failed ($n = 5$). Stem-to-nest and nest-opening angles were distinct ($P < 0.001$ for all four) but did not differ between successful and depredated nests (stem to nest: $F_{1,63} = 0.47$; $P > 0.25$; nest opening: $F_{1,69} = 2.9$; $P > 0.05$).

Table 10. Species with the five greatest importance values determined by foliage hits in the shrub and tree layers at Altamira Oriole nest plots ($n = 30$) and non-use plots ($n = 30$) at Bentsen-Rio Grande Valley State Park, Texas, 2002-2003. Only nests that were within park boundaries are included here. D = density, or total number of foliage hits; RD = relative density (%); F = frequency of plots that had foliage hits of the species (%); RF = relative frequency (%); IV = importance value.

Species	Common name	D	RD	F	RF	IV
Tree layer (>3 m)						
Nest plots						
Ulmus crassifolia	cedar elm	755	33.8	63.3	17.4	51.2
Celtis laevigata	sugar hackberry	540	24.2	70.0	19.3	43.4
Acacia minuata	huisache	194	8.7	26.7	7.3	16.0
Prosopis glandulosa	mesquite	122	5.5	30.0	8.3	13.7
Tillandsia usneoides	Spanish moss	127	5.7	26.7	7.3	13.0
Non-use plots						
Celtis laevigata	sugar hackberry	566	18.6	53.3	11.6	30.2
Prosopis glandulosa	mesquite	520	17.1	53.3	11.6	28.7
Ulmus crassifolia	cedar elm	441	14.5	46.7	10.1	24.6
Celtis pallida	granjeno	237	7.8	63.3	13.8	21.5
Acacia minuata	huisache	342	11.2	33.3	7.2	18.5
Shrub layer (1-3 m)						
Nest plots						
Ulmus crassifolia	cedar elm	442	26.8	43.3	8.9	35.7
Celtis pallida	granjeno	345	20.9	56.7	11.6	32.6
Celtis laevigata	sugar hackberry	121	7.3	53.3	11.0	18.3
unidentified grass	unidentified grass	44	2.7	53.3	11.0	13.6
Zanthoxylum fagara	colima	86	5.2	30.0	6.2	11.4
Non-use plots						
Celtis pallida	granjeno	897	34.2	86.7	14.5	48.7
Cocculus diversifolius	snail seed	168	6.4	60.0	10.1	16.5
Ulmus crassifolia	cedar elm	223	8.5	43.3	7.3	15.8
Condalia hookeri	brasil	225	8.6	36.7	6.1	14.7
Prosopis glandulosa	mesquite	129	4.9	36.7	6.1	11.1

Table 11. Species with the five greatest importance values determined by foliage hits in the shrub and tree layers at Altamira Oriole nest plots ($n = 13$) and non-use plots ($n = 13$) at Santa Ana National Wildlife Refuge, Texas, 2002-2003. Only nests that were within refuge boundaries are included here. D = density, or total number of foliage hits; RD = relative density (%); F = frequency of plots that had foliage hits of the species (%); RF = relative frequency (%); IV = importance value.

Species	Common name	D	RD	F	RF	IV
Tree layer (>3 m)						
Nest plots						
Celtis laevigata	sugar hackberry	262	19.2	76.9	14.9	34.1
Acacia minuata	huisache	284	20.8	53.8	10.4	31.2
Ulmus crassifolia	cedar elm	230	16.8	61.5	11.9	28.8
Bumelia celastrina	la coma	96	7.0	23.1	4.5	11.5
Parkinsonia aculeata	retama	61	4.5	30.8	6.0	10.4
Non-use plots						
Ulmus crassifolia	cedar elm	240	17.3	53.8	10.9	28.2
Parkinsonia aculeata	retama	245	17.7	46.2	9.4	27.0
Acacia minuata	huisache	174	12.5	38.5	7.8	20.4
Prosopis glandulosa	mesquite	163	11.8	23.1	4.7	16.4
Celtis laevigata	sugar hackberry	84	6.1	30.8	6.3	12.3
Shrub layer (1-3 m)						
Nest plots						
Celtis pallida	granjeno	201	13.0	53.8	6.4	19.3
Celtis laevigata	sugar hackberry	148	9.5	69.2	8.2	17.7
Ulmus crassifolia	cedar elm	133	8.6	61.5	7.3	15.8
Cocculus diversifolius	snail seed	148	9.5	38.5	4.5	14.1
Diospyrus texana	Texas persimmon	109	7.0	38.5	4.5	11.6
Non-use plots						
Celtis pallida	granjeno	173	14.5	53.8	8.1	22.6
Parkinsonia aculeata	retama	99	8.3	38.5	5.8	14.1
Zanthoxylum fagara	colima	90	7.5	38.5	5.8	13.4
Cocculus diversifolius	snail seed	88	7.4	38.5	5.8	13.2
Serjania brachycarpa	serjania	63	5.3	46.2	7.0	12.3

Table 12. Species with the five greatest importance values determined by foliage hits in the shrub and tree layers at Altamira Oriole nest plots (*n* = 9) and non-use plots (*n* = 9) at La Joya tract, Lower Rio Grande Valley National Wildlife Refuge, Texas, 2002-2003. Only nests that were within refuge boundaries are included here. D = density, or total number of foliage hits; RD = relative density (%); F = frequency of plots that had foliage hits of the species (%); RF = relative frequency (%); IV = importance value.

Species	Common name	D	RD	F	RF	IV
Tree layer (>3 m)						
Nest plots						
Celtis laevigata	sugar hackberry	213	31.1	88.9	20.0	51.1
Fraxinus berlandieriana	Mexican ash	118	17.3	66.7	15.0	32.3
Leucaena pulverulenta	tepeguaje	128	18.7	33.3	7.5	26.2
Ulmus crassifolia	cedar elm	76	11.1	33.3	7.5	18.6
Taxodium mucronatum	bald cypress	64	9.4	22.2	5.0	14.4
Non-use plots						
Celtis laevigata	sugar hackberry	460	61.0	77.8	26.9	87.9
Cocculus diversifolius	snail seed	71	9.4	55.6	19.2	28.6
Acacia minuata	huisache	121	16.0	33.3	11.5	27.6
Parkinsonia aculeata	retama	48	6.4	33.3	11.5	17.9
Clematis drummondii	old man's beard	11	1.5	22.2	7.7	9.2
Shrub layer (1-3 m)						
Nest plots						
Celtis laevigata	sugar hackberry	48	15.6	66.7	12.8	28.4
Ulmus crassifolia	cedar elm	61	19.9	44.4	8.5	28.4
Leucaena pulverulenta	tepeguaje	25	8.1	44.4	8.5	16.7
Arundo donax	arundo	29	9.4	33.3	6.4	15.8
Salix negra	black willow	26	8.5	22.2	4.3	12.7
Non-use plots						
Celtis laevigata	sugar hackberry	176	37.8	77.8	20.0	57.8
Celtis pallida	granjeno	94	20.2	33.3	8.6	28.8
Acacia minuata	huisache	54	11.6	33.3	8.6	20.2
Cocculus diversifolius	snail seed	27	5.8	44.4	11.4	17.2
unidentified vine	unidentified vine	27	5.8	33.3	8.6	14.4

Table 13. Habitat variables associated with successful and depredated Altamira Oriole nests in the Lower Rio Grande Valley, Texas, USA, 2002-2003.[a] Means with asterisks denote a significant difference (Univariate Logistic Regression, Likelihood Ratio χ^2 Statistic) between successful and depredated nests. Mean angles were tested for differences using the Watson-Williams test (Zar 1996), but neither of the two groups were different.

	Successful				Depredated		
Variables	$\overline{X}$ [a]	SE	n [b]		$\overline{X}$ [a]	SE	n [b]
Nest-placement variables							
Nest height (m)	9.0*	0.3	46		8.2*	0.5	25
Nest tree height (m)	12.9	0.4	42		12.3	0.5	23
Nest tree dbh (cm)	31.2	1.3	42		33.2	2.3	23
Stem to nest distance (m)	5.2*	0.3	42		5.8*	0.3	23
Concealment	7.8*	0.9	46		9.8*	1.6	25
Stem to nest angle (°)	310.4	-	42		317.0	-	23
Nest opening angle (°)	294.4	-	46		315.3	-	25
Nest-site variables							
% canopy cover	46.0	2.7	46		40.9	4.4	25
Large trees, 15-30 cm dbh	0.8	0.1	46		1.0	0.2	25
Small trees, >30 cm dbh	3.2	0.3	46		2.8	0.4	25
Snags	1.7	0.3	46		1.3	0.4	25
Logs	4.6***	0.6	46		2.2***	0.6	25
Max. veg. height	12.2*	0.3	46		11.4*	0.5	25
Height variation	2.6	0.2	46		2.5	0.2	25
foliage frequency, 0-1m (%)	87.5	3.2	46		84.0	4.4	25
foliage frequency, 1-3m (%)	48.1	3.9	46		41.9	4.3	25
foliage frequency, >3m (%)	57.1	3.2	46		56.4	4.0	25
Foliage density, 0-1m	138.1	7.9	46		124.2	10.4	25
Foliage density, 1-3m	81.5**	10.0	46		51.5**	6.6	25
Foliage density, >3m	87.9	7.2	46		79.7	7.3	25
Vert. structural div. (VSD)	2.4	0.1	46		2.5	0.1	25

[a] Significant Likelihood Ratio Test: *$P < 0.25$ for inclusion in the multivariate logistic regression; **$P < 0.05$; ***$P < 0.01$.

[b] Sample sizes varied because six nests on power lines had no supporting tree to measure.
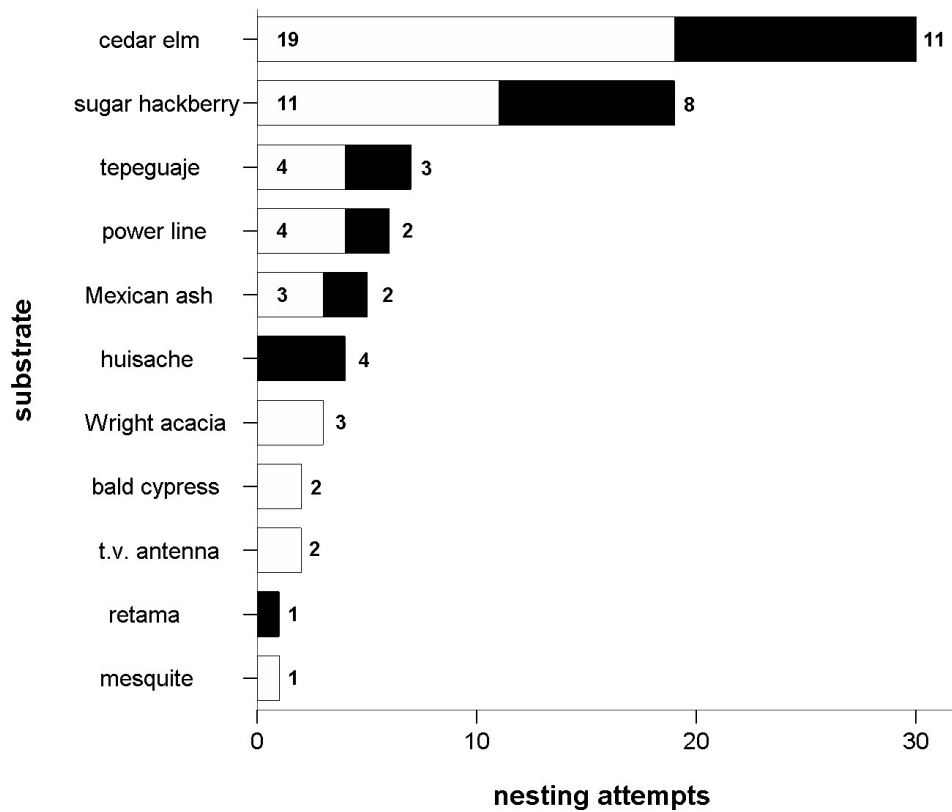
Figure 8. Altamira Oriole nesting substrates with known outcome during 2002-2003 (*n* = 80), including nesting attempts in reused nests. White sections in the bars represents successful attempts and dark sections indicate failed attempts. For Wright acacia, bald cypress and television antenna, the same tree or antenna was used for all of the respective nesting attempts during both years.

DISCUSSION

CURRENT BREEDING STATUS AND HISTORICAL TRENDS

Bentsen. Bentsen-Rio Grande Valley State Park currently has the greatest number of Altamira Oriole nests of the major brush tracts in the middle portion of the LRGV. Brush (1996) located 28 nests during 1993-1995, an average of 9.3 nests per year. This is about half of my average of 18.5 nests per year (Table 3). My search effort was greater, and four nests during 2002-2003 were located beyond park boundaries in areas that Brush may not have searched. But even with the lack of standardization between these two studies, the number of nests in 2002-2003 was probably higher (certainly not lower) than during 1993-1995. This assertion is also somewhat supported by the CBC data, although it is unclear how much of the area was sampled during the CBC counts.

   Santa Ana. The 10 breeding pairs and 17 nests at Santa Ana in 2003 suggests a much larger present-day breeding population than those found by Brush (1996; average of five nests per year during 1993-1995), and a somewhat larger population found by Hathcock and Brush (2004; average of nine nests per year during 1997-1999). But 10 pairs is still fewer than the 15 to 20 pairs that Gehlbach (1981) reported regularly breeding at Santa Ana during the late 1960s and early 1970s. There were several large stands of elm-hackberry forest in the northwestern and eastern parts of Santa Ana that I was not able to adequately survey, which may contain additional nesting sites. It is unclear how comparable the CBC data are to the actual numbers of orioles at Santa Ana. Because of the large amount of habitat away from roads and trails at Santa Ana, CBC data probably do not reflect a complete measure of the nesting population.

Hathcock and Brush (2004) noted a long-term shift in locations of Altamira Oriole nests at Santa Ana from 1974 to 1999. Pleasants (1977) found orioles nesting more or less throughout Santa Ana in 1974, but most of the nests during 1997-1999 found by Hathcock and Brush (2004) were located along the Rio Grande and near the wetlands in the northern section of Santa Ana (Figure 9). Many of the oriole nests that I found followed a similar spatial pattern found by Hathcock and Brush, but I had fewer nests along the Rio Grande in the eastern section of Santa Ana. Many of the nesting sites found by Pleasants have degraded into thorn scrub and bear little if any resemblance to typical oriole nesting habitat (S. M. Werner, personal observation). However, many areas in the southern half of Santa Ana (Mesquite, Owl, Resaca, southern Jaguarundi, and Vireo Trails) have scattered large trees that appear to be suitable oriole nesting habitat. The oriole nests found in 2003 off Jaguarundi trail (Figure 9) were close to nesting areas during 1974 (Pleasants (1977), but no nests were found there during 1997-1999 (Hathcock 2000). This could mean that orioles are slowly re-colonizing the area. However, the year-to-year oriole distribution has probably varied. Castillo (1997) found orioles in this area during his year-round 1995-1997 surveys on Owl and Resaca trails, but he did not provide the time of year of the observation(s) or any other details about the orioles detected.

I found orioles nesting in an area of Santa Ana where oriole nests were present during 1973-1978 but absent during 1995-1996. Cantu (1996) and Brush and Cantu (1998) found no Altamira Oriole territories in 1995 and 1996 on survey plots where Gehlbach (1987) observed nests during 1973-1978. After comparing his vegetation data
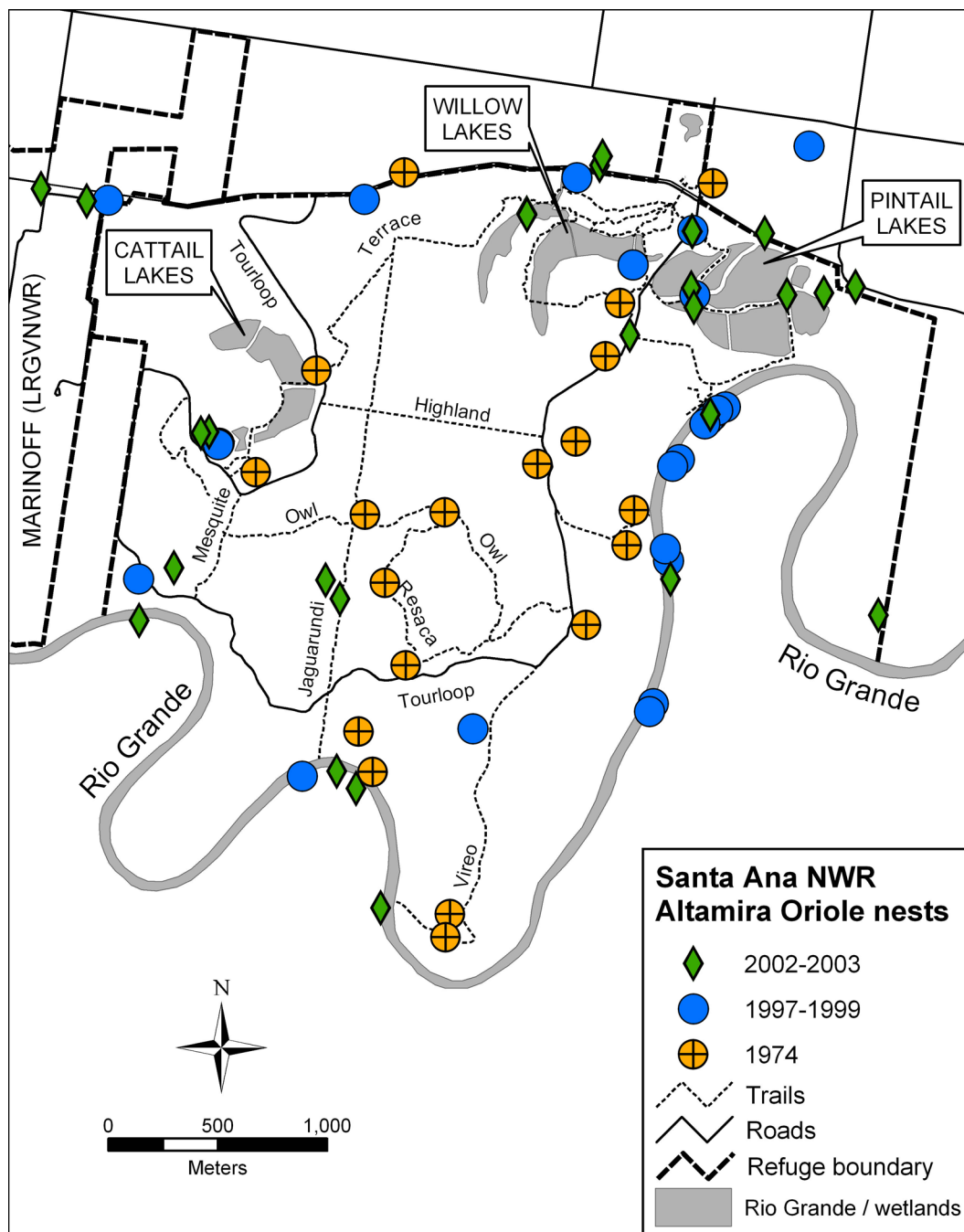
Figure 9. Nest locations of Altamira Oriole nests at Santa Ana National Wildlife Refuge and Marinoff tract of the Lower Rio Grande Valley National Wildlife Refuge during 1974 (*n* = 19; Pleasants 1977), 1997-1999 (*n* = 26; Hathcock 2000), and 2002-2003 (*n* = 29; this study). There were approximately 11 additional nests in 1974 that are not plotted here (Webster 1974), but the 1997-1999 and 2002-2003 efforts included all or nearly all completed nests on the refuge during those years.

with Gehlbach's notes, Cantu (1996) noted that this area (along the tour loop south of Willow and Pintail Lakes) had changed from a tall forest dominated by tepeguaje and Texas ebony, to a shorter, thornier woodland where tepeguaje density was 2 trees per ha. Tepeguaje is still mostly absent in this area (S. M. Werner, personal observation) but a pair of subadult Altamira Orioles nested on a power line in the northern section of Gehlbach's and Cantu's study plots. Cantu was probably seeing the low oriole densities at Santa Ana also noted by Brush (1996) during his 1993-1995 surveys. Brush and Cantu (1998) noted that orioles wintered in this northern section but moved out during the breeding season, while Gehlbach (1987) observed the opposite: orioles nested there but were absent from December to March. It is unclear if this area has been favorable to orioles throughout the time span discussed here, or if the habitat was unfavorable during the 1990s and has now "recovered." Future studies that further replicate those of Cantu (1996) and Gehlbach (1987) would provide valuable information about long-term changes in the vegetation and avian communities of this location.

Other sites. Orioles did not nest at Madero in 2003 after nesting there in 2002. Any orioles still in the area in 2003 could have nested in unexplored parts of Madero tract or in nearby residential or scattered woodland areas such as La Lomita Mission (Figure 5). The nests found in the Madero residential area indicate that Altamira Orioles are adaptable to human settlements (see below: Nest-site selection and nesting success). No orioles were found during either year at Anzalduas County Park, where they nested as recently as 1999 (T. Brush, University of Texas – Pan American, unpubl. data). The interior of Gabrielson likely supports more orioles than just the one pair found in 2003,

because there is extensive, tall thorn forest that looks very similar to parts of Santa Ana. Gabrielson, Madero tract, and Anzalduas County Park will probably have tall forests capable of supporting Altamira Orioles for the foreseeable future because of high soil moisture provided by Anzalduas Dam.

La Joya probably supported similar numbers of orioles during 2002-2003 as it did during 1996-1997, when Rupert (1997) found 10 oriole nests there. She surveyed the riparian strip on the western side of the tract, and I concentrated on the strip on the eastern side (Figure 5). The two areas have similar habitat: riparian forest dominated by sugar hackberry and Mexican ash. After finding two oriole nests built in tepeguajes in an upland area during 2002, there were no nests in that location in 2003. For whatever reason, it may not have been advantageous to nest in the tepeguaje. The first of the 2002 nests failed and the outcome of the re-nesting attempt was unknown. If either of these birds attempted to nest in 2003, the nest location could have been in the riparian strip, because there was an additional breeding pair in this strip during 2003.

PRESENCE OF SUBADULTS IN THE BREEDING POPULATION

The large number of breeding subadults in this study population appears to be a novel phenomenon in Altamira Orioles. This species was not known to breed in its second year until Brush (1996) noted some casual observations at sites in Starr and Cameron counties and was unable to determine the outcome of the nests. Prior to 1996, authors of Altamira Oriole literature either make no mention of breeding subadults or state that subadults do not breed (e.g., Dickey and van Rossem 1938, Sutton and Pettingill 1943, Skutch 1954, Pleasants 1977, 1981, 1993, Gehlbach 1987), and to date, this aspect of

Altamira Oriole biology has only been documented in the LRGV (Brush 1996, 1998a, Hathcock 2000).

Brush (1996) saw no nests at Santa Ana and Bentsen tended by subadults, but I observed several nests tended by subadults at those study sites (Table 4). Twenty-one percent (six of 28) of the Altamira Oriole breeding pairs monitored by Hathcock (2000) were composed of at least one subadult. During 2002-2003, I saw a slightly higher proportion of 28%. There are surprisingly few studies that have investigated subadult breeding in oriole species (*Icterus*), a trait that is more common among temperate oriole species (e.g., Sealy 1980). One explanation for the large proportion of currently breeding Altamira Orioles in the LRGV is that after the population reached a low during the late 1980s and early 1990s, natural selection may have favored breeding during the second year if enough subadults were successful at finding newly available territories and producing offspring. Selander (1965), giving a similar hypothesis, stating subadult males might breed when adult male mortality has been high or when favorable environmental conditions make an abundance of breeding habitat available. The greater number of breeding subadult females than breeding subadult males observed in this study suggests that breeding by subadults could have also occurred at some threshold sex ratio in the adult population.

Most investigations into the evolution of delayed plumage maturation have focused on sexually dichromatic species (e.g., Selander 1965, Rohwer et al. 1980, Flood 1984, Foster 1987, Enstrom 1992), in which second-year females breed but second-year males generally do not. Dichromatic species often have temperate distributions, and

many dichromatic species have evolved polygamous mating systems (Lack 1968), but little work has been done regarding delayed maturation of monochromatic, monogamous species such as the Altamira Oriole. Altamira Orioles have probably evolved delayed maturation in a process illustrated by the sexual selection hypothesis (Lack 1954, Selander 1965, Rohwer et al. 1980). This hypothesis states that second-year individuals should maximize survival until their third year, by which time they will have the experience and strength to breed and defend territories. Evolution will have favored individuals that have avoided territoriality in their second year, for which energetically expensive, bright plumage would presumably be needed.

In this study, subadults still held territories, but it was not clear how aggressive they were toward adult males. Some of the breeding pairs composed of two subadults were found in potentially suboptimal habitats such as the recently replanted agricultural fields on El Morillo Banco and La Joya. Because of the insularity of the native brush tracts, there are probably distinct patches of high quality territories and lower quality territories, the former of which would be held by older, more experienced orioles. Subadult pairs were able to fledge young, albeit at a lower rate than adults. Subadult and adult pairs appeared to be equally prone to raise cowbirds. Further research is needed on why subadult Altamira Orioles are suddenly breeding in the LRGV, and similar cases elsewhere in their range should be sought out and studied.

NEST-SITE SELECTION AND NESTING SUCCESS

Nest-site habitat. Altamira Orioles placed their nests in microhabitats that had taller trees, more logs, and reduced canopy cover (probably because of the open space around

the nest). Logs were a predictor of a preferred nest-site, suggesting that orioles prefer to nest in areas with higher levels of recent tree mortality, but with larger trees as well. Successful nests were also located in areas with more logs than depredated nests. But shrub-layer foliage density was higher at successful nests than at depredated nests, when at the same time orioles seemed to be selecting microhabitats with less shrub-layer foliage density for their nests. If a very open shrub layer allows predators to more easily locate the nest (e.g., Martin 1993), natural selection should favor the selection of a nest-site with a denser shrub layer. Similar shrub-layer foliage densities at successful nests and non-use plots suggest that either this parameter is not related to fitness, or that some orioles are nesting in areas that are too open, and are paying a fitness cost because of higher predation rates in those more open habitats. Furthermore, if these LRGV sites are indeed becoming denser in the shrub layer as suggested by Brush and Cantu (1998), perhaps this is a beneficial habitat feature for Altamira Orioles, as long as there is a large tree in which to nest.

The idea that orioles prefer to nest in more broken up, scattered woodlands with higher recent tree mortality makes sense considering their range expansion in the LRGV in the late 1950s, after Falcon Dam eliminated the upstream source of floodwaters to the lower valley and delta. Many areas dried out and turned into thorn scrub at after this event (Oberholser 1974). Unfortunately, the data that exist about Altamira Orioles and their nesting habitat in the LRGV during this time period is anecdotal at best. Brush (1996) indicated that Altamira Orioles have probably benefited from some of the habitat destruction and degradation in the LRGV during the past 50 years. He referred to

Bentsen in particular, where orioles had recently begun nesting in an area along the Rio Grande Hiking Trail that had once been dense forest but was now an open sugar hackberry woodland. Orioles nested here in 2001-2003 (Figure 3), and trees continued to die and fall down during this time.

Brush (1998a) characterized Altamira Orioles as an "edge" species and it is well-known that they prefer open, often secondary-growth woodlands with scattered trees throughout their range (Dickey and van Rossem 1938, Skutch 1954, Howell and Webb 1995). The recent range expansion in the LRGV may not be surprising considering that Dickey and van Rossem (1938:526) noted range expansions in El Salvador, where "the clearing of the forest on mountain slopes has permitted both the mimosa and, following it, the [Altamira] orioles to reach 4,500 feet on both the volcanoes of Santa Ana and San Salvador, although under primitive conditions such an elevation is far above the normal ranges of either." In fact, the use of power lines for nesting by Altamira Orioles was noted in early species accounts (Dickey and van Rossem 1938, Sutton and Burleigh 1940).

Preferred microhabitat. If a site appears suitable for nesting to an oriole, the presence of a flexible branch on the opposite side of the tree from prevailing winds is important as well, as noted by previous authors (Pleasants 1981, Brush 1998a, Hathcock and Brush 2004). Gusty winds are common in spring and summer in the LRGV, and heavy thunderstorms and tropical storms may appear at any time during June and July (although wind directions may change temporarily with such storms). Only two of the 83 nesting attempts monitored failed due to a branch breaking. One of these, built by an

adult female, was in a tree used during each of the previous two years and was on a branch oriented at 318 degrees, almost perfectly in line with the average wind direction of 136 degrees. But the limb was apparently dead and not flexible enough. The second nest that fell was built by a subadult female in a dead cedar elm that had no major limbs remaining and was essentially one large, dead stem whose end overhung an open area. Given the brittle look of the tree, I was not surprised when I saw that the nest had fallen. The orientation of the nest was 25 degrees, and the lateral stress to the branch probably caused it to break. Apparently, dead supporting branches can also break when heavy rains weigh down a nest (Webster 1962), which is a common source of nest mortality in Montezuma Oropendolas (*Psarocolius montezuma*), whose nests are at least twice as large as Altamira Oriole nests (Webster 1994).

A further risk of preferring areas that have dying trees is that the chosen nest tree may be not be structurally sound as a whole. A nest at Santa Ana in an 8-m-tall sugar hackberry failed because the tree trunk broke about 1.5 m above the ground, causing the entire tree to fall down. At Bentsen, orioles built nests during both 2002 and 2003 in the same dead cedar elm, apparently on the same branch. The 2002 nest failed during egg-laying and fell to the ground less than 10 days later, after the support twigs broke. In 2003, however, the nest built in this dead cedar elm remained intact and fledged at least five young. This, along with other successful nests in a dead mesquite and a dead Mexican ash, suggests that the benefits sometimes out weigh the risks.

A suitable nesting area need not have a suitable nesting-branch, as was shown by the six nests built on either power lines or television antennas. These manmade

structures are much sturdier and probably far less likely to fall down than tree limbs. Guy wires supporting telephone poles are also used for nesting (Brush 1996, S. M. Werner, personal observation) and Brush (1996) observed orioles nesting on an electrical substation superstructure. But nests on power lines can be blown around if they are not fully secured. Brush (1996) monitored several nests under construction that were blown along a power line and disintegrated. In 2002, a nest on a power line at Bentsen whose construction was nearly complete was blown 31 m along the power line until ending up about 1 m from the next support pole. The orientation of the power line was 138 degrees, almost exactly in line with a southeasterly wind coming from 134 degrees. Amazingly, the nest remained intact, and three orioles eventually fledged.

The sturdiness of a power line can also allow a well-built nest to be reused, which happened twice during 2002-2003. The nest in 2002 was successful during both attempts. In 2003, a power-line nest at Bentsen failed early in the nestling stage and was later reoccupied with new eggs approximately 39 days later, after the female had had two more failed nesting attempts nearby. The availability of her previously-built nest, at a time when the bird was forced to attempt a fourth clutch of the season, probably represented a large energetic advantage.

Preferred nest-tree species. Hathcock and Brush (2004) saw a shift in Altamira Oriole nesting trees at Santa Ana from mostly tepeguaje and Texas ebony in the early 1970s to primarily black willow, Mexican ash, and huisache during 1997-1999 (Table 14). The numbers of 2002-2003 nests in black willow, cedar elm, Mexican ash, and sugar hackberry more resemble distributions seen in 1993-1995 than those seen in 1997-

1999. I found fewer nests in large willows and ashes along the Rio Grande than did

Hathcock and Brush. But my search effort was probably less than theirs in that I only

canoed the Rio Grande at Santa Ana once per season. Unfound nests may have fallen

down or could have been built later in the season.

From 1996-1999 none of 48 Altamira Oriole nests and Santa Ana were in

tepeguaje (Hathcock 2000). I found ten nests in tepeguaje (two at Santa Ana), but they

all seemed to be in atypical locations, such as near canals, in residential areas, and in

replanted areas of refuge tracts. It is nonetheless encouraging that orioles are again

using this tree that was once so commonly used for nesting (Hathcock 2000). The

reduction in the number of oriole nests in tepeguaje and Texas ebony seen after 1981

was mostly due to reduced numbers of large individuals of those species (Hathcock and

Brush 2004). Cantu (1996) found that tepeguaje had disappeared by 1995 as the

dominant canopy tree in parts of Santa Ana when he examined plots that were studied by

Gehlbach (1987) during 1973-1978. Severe freezes in 1983 and 1989 destroyed many

large tepeguajes and Texas ebonies in the LRGV, but cedar elm, sugar hackberry, and

Mexican ash, which have more temperate-zone distributions, were more resistant to the

freeze damage (Lonard and Judd 1991). Tepeguajes that supported nests at La Joya and

El Morillo Banco were planted in 1992 and 1993, respectively (C. Best, U.S. Fish and

Wildlife Service, unpubl. data). The lack of a major freeze since 1989 has probably

allowed many tepeguajes to grow into large trees. Currently, some naturally forested

areas within Santa Ana and Bentsen have smaller tepeguajes that might grow larger and

support oriole nests in the future.

Table 14. Tree species used by Altamira Orioles for nesting at Santa Ana National Wildlife Refuge, Hidalgo County, Texas, USA, 1974-2003. Totals for each year do not necessarily reflect total number of nests found on Santa Ana that year.

Tree species	Common name	Number of nests[a]				
		1974[b]	1980-1981	1993-1995	1997-1999	2002-2003
Salix negra	black willow	0	1	4	10	1
Ulmus crassifolia	cedar elm	1	1	6	2	7
Acacia minuata	huisache	2	0	3	5	4
Prosopis glandulosa	mesquite	1	0	0	0	0
Fraxinus berlandieriana	Mexican ash	0	0	1	6	1
Celtis laevigata	sugar hackberry	0	1	6	2	8
Tamarix sp.	tamarisk	0	0	0	0	1
Leucaena pulverulenta	tepeguaje	5	6	0	0	2
Chloroleucon ebano	Texas ebony	2	1	1	1	0

[a] Data sources: 1974, B. Y. Pleasants, unpubl. data; 1980-1981, M. D. Carter, unpubl. data; 1993-1995, Brush (1996); 1997-1999, Hathcock (2000); 2002-2003, this study.

[b] Total number of nests found at Santa Ana in 1974 was 30 (Webster 1974) but tree species data for the others was unavailable.

Nest-site fidelity. Altamira Orioles have been observed nesting in the same tree for 2 to 3 years (Brush 1998a), and I saw several examples of this in my study. Two interesting examples occurred when two nests were built in 2003 in the exact location as in 2002, but by different females. The 2002 females were adults and the 2003 females were subadults. Perhaps these sites appeared favorable to the female, or the small amount of left-over material from the previous year was a sign of the location's usefulness. The territory could have been held over the winter by the male, and perhaps the male helped in choosing the nest-site. Virtually nothing is known about overwinter territorial shifts, juvenile dispersal, and parental roles in nest-site selection of the Altamira Oriole. Most territorial interactions have been observed during November and December (Brush 1998a). Future studies involving marked individuals would undoubtedly shed light on demographic patterns as well as sex-specific behaviors involved in courtship, nest-site selection, and nest-site longevity.

Double-brooding and nest reuse. As noted by Hathcock, many oriole pairs attempted two broods, but after the second brood no further attempts were made. Although I made a large assumption about following unmarked breeding pairs, orioles in this study almost certainly attempted multiple broods, and they did this frequently. In Pleasants' (1993) review, she stated that northern populations of Altamira Orioles raise one brood and southern populations possibly raise two broods. Even though its nest is probably better-protected from predation than other tropical passerines, it seems unlikely that the Altamira Oriole would not attempt a second brood given the climatic stability and long breeding season throughout its range. Great Kiskadees (*Pitangus sulphuratus*),

for example, build enclosed nests that are probably well-protected from predators, and regularly raise two broods (Brush and Fitzpatrick 2002).

It is probably energetically advantageous to reuse nests for seconds broods, as noted above. Nine percent (seven of 76) of nests were reused after an initial brood. One of the failed nests that was eventually reused was located on a power line and I was unable to inspect the condition of the inside of the nest. Future researchers should be aware of the tendency to reuse nests, and they should address the availability of nest sites on territories where pairs reuse their original nest.

NEST PREDATION

Despite its elaborate design, the Altamira Oriole nest is still vulnerable to predators, especially during the laying and incubation stages. During the egg-laying stage, passerines often only visit the nest once per day, to lay eggs (Martin and Geupel 1993), and Hathcock (2000) confirmed that Altamira Orioles leave their nests completely unattended for long periods of time during this stage. I noticed a similar pattern while monitoring nests in this study. In addition, I found that three oriole nests were depredated during the nestling stage, unlike Hathcock (2000), who observed no nest failures during this stage. Daily survival rates from predation during incubation were not different than Hathcock's (2000) data ($\chi^2_1 = 0.0$, $P = 1.0$). However, during the nestling stage I observed three nests that failed due to predation and Hathcock observed no nestling stage losses, which resulted in a significantly different daily survival rate ($\chi^2_1 = 4.0$, $P = 0.046$) between the nestling stage survival rates of the two studies.

Identification of nest predators was lacking in this study and remains a poorly

understood area of Altamira Oriole nesting ecology (Brush 1998a, Hathcock 2000).

Potential predators on open-cup nests on LRGV brush tracts are abundant and diverse

(e.g., Hathcock 2000) but there are probably few predators besides cowbirds that would

be able to enter an oriole nest, especially if the adults are there to defend it (see Nest

Parasitism below). Most snakes are probably not able to enter nests, and Pleasants

(1993) hypothesized that the use of small branches for oriole nests may be an adaptation

against snake predation. Brush (1996) saw an oriole nest near Falcon Dam with its

bottom ripped out that had presumably had been in the nestling stage 18 days earlier.

Inferring the identity of nest predators from nest condition or contents alone is a highly

subjective and inaccurate process (Lariviere 1999). Nonetheless, for a unique nest such

as that of an Altamira Oriole we can probably rule out a certain suite of animals unable

to reach the nest to depredate it. Opossums (*Didelphis virginiana*) prey on bird nests

(Dijak and Thompson 2000**)** and are probably the largest mammalian predator in the

LRGV capable of reaching an oriole nest (although they may be *too* large).

Brush (1996) reported on an incident where an eastern fox squirrel (*Sciurus

niger*) was seen entering an Altamira Oriole nest of unknown status. I saw fox squirrels

in several oriole nest-trees, some of which failed. Smaller rodents can prey upon bird

eggs (Haskell 1995), and Sternberg (2001) inventoried rodent communities at mature

brushland and replanted sites 8 km east of Santa Ana. The rodents he found, listed in

order of abundance, were hispid cotton rat (*Sigmodon hispidus*), white-footed mouse

(*Peromyscus leucopus*), Mexican pocket mouse (*Liomys irroratus*), house mouse (*Mus

musculus*), southern plains woodrat (*Neotoma micropus*), black rat (*Rattus rattus*),

Coues' rice rat (*Oryzomys couesi*), fulvous harvest mouse (*Reithrodontomys fulvescens*), hispid pocket mouse (*Chaetodipus hispidus*), and marsh rice rat (*Oryzomys palustris*). Gehlbach (1981) commented on how house mice had invaded certain parts of Santa Ana after flooding was eliminated.

Robinson (1985) reported that pendulous nests of the Yellow-rumped Cacique (*Cacicus cela*), a South American colonial-nesting icterid, were depredated primarily by brown capuchin (*Cebus paella*), Great Black-hawk (*Buteogallus urubitinga*), Black Caracara (*Daptrius ater*), and Cuvier's Toucan (*Ramphastos cuvieri*). Of these, only the capuchin reached inside the nests to take eggs or nestlings; the avian species tore open the nests. Because none of nests in my study were ripped open, this suggests that none were depredated by large birds. Brown capuchins and Cuvier's Toucans also prey on nests of Casqued Oropendola (*Psarocolius oseryi*; Jaramillo and Burke 1999), and Smith (1983) noted that nest predators of Chestnut-headed Oropendola (*Psarocolius wagleri*) are diverse, including toucans, snakes, opossums, bats, but primarily botfly larvae (*Philornis* spp.). Unfortunately, little is known about nest predation on any of the three pendulous-nesting orioles (Altamira Oriole, Spot-breasted Oriole [*Icterus pustulatus*], and Streak-backed Oriole [*Icterus pectoralis*]) common to Mexico and Central America.

Great-tailed grackles are known to prey on bird eggs and nestlings in the LRGV (Johnson and Peer 2001), although only the females appear small enough to enter an oriole nest. At least four depredated nests were located in areas where I saw heavy grackle activity during the same few weeks that these nests failed. One nest at El Morillo Banco that failed during incubation was located in the same tree as a grackle

nest that contained begging chicks when the oriole nest failed. Large raptors such as gray hawks (*Asturina nitida*), Harris's Hawks (*Parabuteo unicinctus*), White-tailed Hawks (*Buteo albicaudatus*), and Great Horned Owls (*Bubo virginianus*) are probably capable of targeting Altamira Oriole nests, but as mentioned above, may not have been a factor in the nests that I studied. However, an oriole nest at Santa Ana was abandoned while still under construction possibly because a Harris's Hawk started using the nest tree (a black willow) as a consistent perch. Green Jays (*Cyanocorax yncas*) were common at the sites, but there is little evidence that they are nest-robbers, unlike other common North American jays such as Western Scrub-Jays (*Aphelocoma californica*) and Blue Jays (*Cyanocitta cristata*; Gayou 1995).

Nesting associations with other aggressive bird species. Anecdotal evidence suggests that Altamira Orioles sometimes nest near aggressive tyrannids such as Couchs's Kingbird (*Tyrannus couchii*), Great Kiskadee, and Rose-throated Becard, and that this provides additional protection of the eggs and young from predators and cowbirds (e.g., Pettingill 1942, Sutton and Pettingill 1943, Pleasants 1981, 1993, Brush 1998a). Indeed, in the first record of an Altamira Oriole nest in the LRGV, Grimes (1953) noted that a Great Kiskadee nest had been built in the same tree as the oriole nest.

Although I did not do a thorough sampling effort, I was able to count 17 Great Kiskadee nests (which are fairly conspicuous) within 15 m of 79 Altamira Oriole nests. It was often unclear which species began building first (Altamira Oriole or Great Kiskadee). Several oriole nests were located near Couch's Kingbird nests as well. All three of these species clearly nest in large trees at the sites (S. M. Werner, personal

observation). These nesting associations likely confer benefits for orioles but are not necessary for successful oriole nests. Nesting associations of tropical icterids and tyrannids are common (e.g., Fitzpatrick 1983, Smith 1983), and both families have colonial or semi-colonial species. Tropical avian species are also known to nest near wasp nests with fitness advantages (e.g., Joyce 1993). Further research in the LRGV and in the tropics with Altamira Orioles and potential associated nesters could elucidate behavioral patterns and fitness advantages or disadvantages to group nesting for the oriole. Such a study would require monitoring nests and behaviors of all species involved, throughout the breeding season.

COWBIRD PARASITISM AND PREDATION

Records of successful parasitism by Bronzed Cowbirds of Altamira Oriole nests are extremely rare and were mostly anecdotal before the 1990s. Dickey and van Rossem (1938) were told by locals in El Salvador that Bronzed Cowbirds were most-often raised by the three common lowland orioles (*I. gularis, I. pustulatus, I. pectoralis*), but the authors cite no specific examples. In her review, Pleasants (1993) stated that no well-documented cases of Altamira orioles raising cowbirds existed. The first two confirmed reports from the LRGV were in 1996 and 1997 (Brush 1996, 1998a). During his study from 1997-1999, Hathcock (2000) found 1 successfully parasitized nest out of 22 active nests (5%). During 2002-2003, I found roughly the same parasitism proportion (five out of 80, or 6%) in Altamira Oriole nests. Records of Bronzed Cowbird eggs in Altamira Oriole nests are not as rare (Webster 1962, Friedmann 1963, Oberholser 1974, Friedmann et al. 1977), and Bronzed Cowbirds have been seen in or around oriole nests

even if observers could not confirm any cowbird egg-laying (Pleasants 1981, Carter 1986). In this study I did not estimate rates of cowbird parasitism because many nests were inaccessible and those that I did inspect were not inspected regularly enough to give accurate estimates.

Despite the fact that very few Bronzed Cowbirds are raised by Altamira Orioles, and that orioles can fledge their own young along with Bronzed Cowbirds (as shown in this study), Bronzed Cowbirds could have an underestimated effect on oriole productivity in the form of egg piercing. Bronzed Cowbirds often pierce another egg in the nest before laying one of their own (Carter 1986). Although orioles are capable of removing Bronzed Cowbird eggs (Hathcock 2000), multiple parasitism events can quickly eliminate an oriole clutch, especially if host eggs are damaged during removal of cowbird eggs (see below). Dump nests, such as the one I observed with four Bronzed Cowbird eggs, may not affect orioles if no host eggs are pierced because of orioles' ability to remove cowbird eggs. However, if an oriole loses its entire clutch, building another large, pendulous nest probably represents a greater energetic expenditure than that of other, open-cup nesting cowbird hosts upon re-nesting (but see *Double-brooding and nest reuse* above).

In this study I observed a large number of partial-clutch losses (17 in 12 different nests), each of which could have resulted from egg-piercing by Bronzed Cowbirds and then egg-removal by an oriole before my subsequent inspection. Individual egg losses in this study resulted in a partial difference between an initial mean clutch size of 3.9 ($n = 30$) eggs and a mean number of young fledged of 2.4 ($n = 14$), among precisely-known

nest contents. Hathcock (2000) observed only 1 partial clutch loss out of 25 oriole nests monitored during incubation, and he observed a clutch size of only 2.7 ± 0.2 ($n = 9$). Further data is needed on whether cowbirds indeed have an effect on partial clutch losses such as those observed in this study.

I found that failed nests had more cowbird visits per hour than successful nests, but there was much larger variability in the visitation rate to failed nests. Future behavioral studies of cowbirds and orioles could incorporate more standardized methods by using remote 24-hour video cameras. But rather than just concentrating on the number of cowbird visits to oriole nests on any given day, future work could take a more proactive approach of determining which cowbird individuals return to nests the next morning to lay an egg, after presumably scoping out potential nests during the previous day. Because they have been observed to lay eggs just after dawn, female Bronzed Cowbirds are assumed to spend much of the rest of the day seeking out available nests (containing eggs) for future parasitism attempts, but there are no studies that have documented this precise behavior (Lowther 1995).

Clutch size can also be reduced when a host attempts to remove a cowbird egg but damages one's own egg, as Rothstein (1977) and Sealy and Neudorf (1995) showed with Baltimore orioles (*Icterus galbula*) and Bullock's orioles (*Icterus bullockii*). Orioles usually must use their bill to spike or break into pieces the cowbird egg, in order to remove it. Thrusting movements of the bill can miss or be deflected onto their own eggs, causing breakage and thus egg mortality. I may have observed this at the two nests where cowbird eggs had disappeared. When I inspected the nests and saw that the

cowbirds eggs were gone, there was at least 1 broken oriole egg in each nest. At the first nest, the broken oriole egg was the last one remaining and the nest failed, although the parents still defended the nest during my visit. In the other nest, the cowbird egg removal occurred just as incubation began, and two of the five oriole eggs appeared broken. However, 1 of the 'broken' eggs remained in the nest and its apparent puncture may have just been yolk from the other broken egg. I was unable to determine if this egg hatched. Three of the four eggs later hatched, and three young fledged.

Bronzed Cowbirds lay indiscriminately, although early authors suggested that they specialize on orioles (Dickey and van Rossem 1938; Friedmann 1929, 1971; Carter 1986; Hathcock 2000). While most Altamira Orioles probably eject cowbird eggs, an egg that survives to hatching would undoubtedly be benefited by the orioles' high nestling survival rate. The difference in the predation risk of an oriole nest containing only orioles compared to a nest with loud, begging cowbird chicks may be negligible, because the safety of the pendulous nest probably overrides the risk of being too loud.

Cowbird eggs could have gone undetected in this study for several reasons. First, Bronzed Cowbirds can lay their eggs 20 or more minutes before sunrise (Peer and Sealy 1999), and nests in this study were visited at all times of the day. Efforts were made to visit nests early in the morning, but early morning was also a good time of day to find new nests. Sites along the Rio Grande are extremely dangerous to visit during non-daylight hours because of illegal U.S.-Mexican border activity, and I was advised by USFWS and U. S. Border Patrol to work only during daylight hours. Second, nests could not be inspected every day because of limited personnel, and only 1 camera was

available during each season. The majority (19 of 36) of nesting attempts inspected with

the camera before the nestling stage were inspected just three or fewer times. Third, not

all nests could be inspected with the camera because they were either too high or

otherwise inaccessible. Some early 2002 nests were not visited frequently enough, if at

all, because of concerns for the nests' safety and my lack of experience with the camera.

Finally, use of the camera was limited by adverse environmental conditions such as rain,

high winds, and glare from the sun around midday.

Cowbird presence at the study sites. I agree with Hathcock (2000) that none of

the study sites was any less prone to cowbirds. In my study, Bronzed Cowbirds were

fairly common at all the nest sites. Radio-tracking studies of Bronzed Cowbirds (Carter

1984) and Brown-headed Cowbirds (Rothstein et al. 1984) have shown that these two

species have large home ranges (as large as 336 ha and 1000 ha, respectively) compared

to the size of the tracts that I studied in the LRGV (see Table 1). Therefore, cowbirds

can likely exploit most or all of the area within the protected tracts.

FUTURE RESEARCH AND CONSERVATION PRIORITIES

I was able to show that Altamira Oriole population numbers are fairly high at Bentsen

and are probably increasing at Santa Ana, that orioles nest in the largest trees, and that

orioles are susceptible to cowbird parasitism. Despite these findings, much remains

unknown about these oriole populations, such as causes of nest predation and egg loss,

foraging ecology, and why such a large number of breeding subadults has been

observed, and is still growing, over the past 10 years. I was not able to study the

Altamira Oriole population along the 21-km stretch of the Rio Grande just below Falcon

Dam, in Starr County. The dynamics and composition of this population could be different than at the sites I surveyed because the habitat below Falcon is upstream from the Rio Grande delta and almost completely linear.

It is unclear whether some aspects of the orioles in this study (e.g., breeding subadults, multiple broods) are typical of Altamira Oriole populations elsewhere because of the small amount of literature that exists. Further research with Altamira Orioles in the LRGV, supplemented by research in Mexico and Central America, will be needed to fully understand Altamira Oriole nesting ecology. Future monitoring of oriole nests will require the use of micro-video cameras like the one used in this study.

Maintaining Altamira Oriole populations in the LRGV will require the continued presence of large trees and the water to support them, which could be difficult given the water demands of the growing urban populations. Artificial flooding at Santa Ana has been successful at sustaining large trees, and orioles used some of those trees in this study. Bentsen is in immediate need of water management. Although the Bentsen oriole population was fairly dense in this study, forested areas continued to degrade, and some trees used for nests in 2001 had fallen over and were gone by 2003. Flooding of the resaca along the border of El Morillo Banco tract and Bentsen will surely allow more trees to flourish along its edges (Figure 3). But flooding should also be attempted on other areas of Bentsen, such as the depression south of the Singing Chaparral trail, the lowlands south and southeast of the dump road, and the depression on the southwestern corner of the west fork of the Rio Grande Hiking Trail. These areas supported tall trees and oriole nest sites in this study. The moister soils in these last two depressions at

Bentsen probably extend into the agricultural field along the river, due west of the Rio Grande Hiking Trail. This parcel, if acquired and replanted, might support large trees and supplement the existing corridor.

The causes of tree mortality may go beyond a simple lack of water, and there may be tree-disease issues to explore. At some sites large trees died or had rotten trunks while nearby individuals seemed to be faring well. Many of the dying trees were cedar elms and sugar hackberries, which are related (family Ulmaceae), and disease is a possible issue that deserves to be looked at (D. Blankinship, U.S. Fish and Wildlife Service, personal communication).

Restoration of the La Joya and El Morillo Banco tracts has likely benefited orioles with additional nesting sites and foraging areas. As the LRGVNWR grows and more land is restored, use of the newly available habitats by orioles (and other wildlife) should be monitored. Even with the current configuration of refuge tracts, issues such as quality of the nesting habitat, dispersal rates, and predator community composition would be extremely helpful for the future conservation of Altamira Orioles.

CHAPTER IV

NESTING SUCCESS AND NEST-SITE SELECTION

OF THE NORTHERN BEARDLESS-TYRANNULET

INTRODUCTION

The Lower Rio Grande Valley of Texas (LRGV; consisting of Cameron, Hidalgo,

Willacy, and Starr counties) supports a highly diverse flora and fauna and represents the

northernmost range limit of many tropical species (Clover 1937, Blair 1950, Oberholser

1974, Jahrsdoerfer and Leslie 1988). Clearing of subtropical evergreen forest, riparian

woodland, and scrublands (collectively referred to as Tamaulipan brushland, or

brushland) for agricultural and urban needs in the LRGV since the 1920s has resulted in

at least a 95% percent loss of native habitat (Marion 1974, Jahrsdoerfer and Leslie

1988). After a disastrous freeze in 1951, expansive citrus orchards were largely replaced

with row crops, accelerating the landscape transformation and probably hastening the

decline of many wildlife species (Oberholser 1974, Gehlbach 1981). Sennett (1878)

described large tracts of forest and the Spanish moss (*Tillandsia usneoides*) that was

"everywhere provokingly abundant on the larger growth of trees," but large stands of

mossy forests are now rare in the LRGV. Similarly high losses of native habitat are

estimated to have occurred on the coastal plain of adjacent Tamaulipas, Mexico

(Jahrsdoerfer and Leslie 1988).

Even in protected areas, plant communities have been altered by the elimination

of large-scale flooding due to significant water diversions along the Rio Grande such as

Falcon Dam, completed in 1953. Many areas once characterized as subtropical evergreen forest and riparian forest have shifted to thorn-forest and thorn-scrub communities, accompanied by shifts in avian communities (Oberholser 1974, Gehlbach 1981, Brush and Cantu 1998). Severe freezes and droughts have also affected local plant and animal communities (Lonard and Judd 1991, Eddy and Judd 2003, Hathcock and Brush 2004).

The Northern Beardless-Tyrannulet is listed as threatened on State of Texas Threatened and Endangered Species List (Campbell 1995). The U.S. Geological Survey has identified it as one of nine LRGV landbirds with high conservation value for the Species at Risk research program (U.S. Geological Survey 2000). The Northern Beardless-Tyrannulet inhabits arid to semi-humid woodlands, deciduous forest, gallery forest edges, and riparian thickets throughout its range, which extends from southeastern Arizona, southwestern New Mexico, and deep South Texas southward throughout Central America to Costa Rica (Stiles and Skutch 1989, Howell and Webb 1995, American Ornithologists' Union 1998, Tenney 2000). It is a year-round resident species throughout its range, although some populations may make seasonal elevational movements.

The Northern Beardless-Tyrannulet (hereafter, tyrannulet) is considered common to fairly common in most of Mexico from sea level to 2100 m (Howell and Webb 1995). In southern Texas, the tyrannulet has never been considered common, and it has evidently become much rarer in the LRGV since 1951,when the destruction of forests thick with the epiphytic bromeliads ball moss (*Tillandsia recurvata*) and Spanish moss

(*T. usneoides*) accelerated (Oberholser 1974, Brush 1999). Tyrannulets may have increased in Kenedy County just north of the LRGV, because Fall (1973) noted that tyrannulets were typically found in live oak (*Quercus virginiana*) forests, a cover type that had increased during the previous 100 years. In the LRGV tyrannulets are restricted to tracts of native vegetation with tall trees and *Tillandsia*, which have been reduced to a few "islands" of habitat, but virtually no data exist on long-term trends. Tyrannulet populations in coastal Mexico and El Salvador have noticeably decreased in regions with high rates of deforestation (Tenney 2000).

Even though Northern Beardless-Tyrannulets are widespread throughout Central America many aspects of their breeding biology remain unknown (Ehrlich 1998, Tenney 2000). There have been no published data quantifying lengths of incubation and nestling stages and habitat selection. Much of what we know comes from observers in Southeast Arizona (e.g., Vorhies 1935, van Rossem 1936, Anderson and Anderson 1948, Brandt 1951, Philips et al. 1964) and from a recent study in the LRGV (Brush 1999), who noted that the 11 nests described in his study were the first published records of nests in the LRGV since 1940. The nest is a domed or globular structure with a side hole, often concealed in tent caterpillar webs, mistletoe, or, in southern Texas, ball moss and Spanish moss (Tenney 2000). Tyrannulets are small and drably colored, and they probably go undetected much of the time, unless the observer knows the unique vocalizations exhibited by males and females (Brush 1999, Tenney 2000).

In this study my objectives were to (1) determine nest success of the Northern Beardless-Tyrannulet, (2) describe the habitat characteristics of nests, (3) describe

differences in nesting habitat between successful and depredated nests, and (4) assess the past, present, and future breeding status of Northern Beardless-Tyrannulet in the study area.

METHODS

STUDY AREA

I conducted primary field work during 2002 and 2003. Study sites were located in Hidalgo County, Texas, which is considered to be in the "middle valley" of the LRGV (Figure 1). Climate is semi-arid and subtropical (Jahrsdoerfer and Leslie 1988) with an average yearly rainfall of 56 cm and average high temperatures exceeding 35 C° in August. September is the wettest month, with 103 mm rainfall, and May and June each receive about 71 mm of precipitation (1961-2001 averages; National Climatic Data Center 2003).

Vegetation at the study sites has been characterized as "Mid-valley Riparian Woodland" and "Mid-delta Thorn Forest" (Jahrsdoerfer and Leslie 1988). Ancient floodways, or resacas, alternating with upland areas supported a mosaic of plant communities within the sites. Some dry resacas with little standing water contained bottomland forests composed of large Mexican ash, cedar elm, and sugar hackberry trees. Upland and transition areas supported drier thorn forest and thorn scrub, consisting of Mexican ash, cedar elm, sugar hackberry, anacua, Texas ebony, tepeguaje, mesquite. Common shrubs and small trees included Texas persimmon, huisache, brasil, lotebush, colima, la coma, and granjeno, often forming impenetrable thickets. Ground-level vegetation was primarily introduced guinea grass, introduced buffel grass, and

several herbaceous and semi-herbaceous broad-leaved species. Plant communities at the study sites are further described by Vora (1990) and Lonard and Judd (2002).

NEST SEARCHING AND MONITORING

I initially scouted potential sites during July and August 2001, at which time I noted any nests, nesting behaviors, family groups, or singing males. I chose Anzalduas County Park, Bentsen, Gabrielson, Madero, and Santa Ana, as focal study sites because they appeared to harbor the most tyrannulets during my preliminary surveys and during a previous study (Brush 1999). With the help of one field assistant in 2002 and two assistants in 2003, I nest-searched from mid-March until mid-August. I also collected data for a nesting study on Altamira Orioles, so effort was split among the two projects.

Territorial pairs were located by following singing males making the *pier-pier-pier* call and/or following females making *pee-uk* calls (Brush 1999, Tenney 2000). I often used roads and trails to initially locate tyrannulets because of the large amount of thick, impenetrable brush at the sites. Nests were found by following behavioral cues (Martin and Geupel 1993) and monitored from a distance with binoculars at least every 3 to 5 days, with more frequent visits during transition periods. I used standard procedures during nest visits to minimize human disturbance (Martin and Geupel 1993). Nesting attempts were considered successful if nests fledged at least one tyrannulet.

I estimated territorial boundaries at the sites by following nesting individuals and keeping track of simultaneously-active nests, although no birds were color-banded. I defined a breeding pair as the same pair nesting on a territory during the same season, although I had no way of knowing if pair bonds between the unmarked birds were

maintained through the whole season. Locations of nests were recorded using a

handheld GPS device (Map 330M; Magellan Corporation, San Dimas, California, USA)

and plotted on digital orthophoto quadrangles (DOQs) using ArcView 8.3 (ESRI 2002).

I also plotted locations of male-female tyrannulet pairs suspected to be nesting, but

whose nests I did not locate, to aid in future research at the sites.

NEST SUCCESS

I calculated daily nest survival rates, standard errors, and nest success according to

Mayfield (1961, 1975) and Johnson (1979). For failed nests, I calculated the fail date as

the half-way point between the last confirmed active date and the date on which the nest

was confirmed not active (Martin et al. 1997). Clutch sizes could not be estimated due

to the enclosed nature of the nests. I was able to occasionally estimate the minimum

number of nestlings inside a nest visually or aurally, but many nests were located too

high in the canopy to make this estimate. The number of fledglings was determined by

observing begging individuals outside of the nest.

HABITAT MEASUREMENTS

I took two groups of measurements at each tyrannulet nest, representing different scales:

(1) nest-placement variables that described local placement of the nest, and (2) nest-site

variables that described the vegetation around the nest at a larger scale than nest-

placement data.

Nest-placement variables. At nests I recorded tree species, nest tree height,

diameter at breast height (dbh) of the nest tree, nest height at nest opening, azimuth from

the nest-tree trunk to the nest ("trunk-to-nest angle"), compass direction of the nest-

opening ("nest-opening angle"), and horizontal distance from the nest-tree trunk to the nest. Compass bearings were corrected for magnetic declination and recorded for true north. Heights below approximately 8.5 m were measured with a telescopic pole, and heights above 8.5 m were measured with a clinometer.

Nest-site variables. I measured vegetation at the nest site using a 0.04-ha circular plot (James and Shugart 1970, Martin et al. 1997) centered at the nest. I used a paired, random-plot design to identify features of the vegetation that were more likely to be associated with oriole nests. The center of the 0.04-ha circular non-use plot was located at a random compass direction and a random distance between 20 and 50 m from each nest. Like nests, non-use plot locations were recorded with the GPS device. The same nest-site variables were measured at all nest plots and non-use plots. I recorded the number, dbh, and species of small trees (dbh 15-30 cm), large trees (dbh > 30 cm), and snags (dbh > 15 cm, height > 1.4 m), and the number of fallen logs (diameter > 15 cm and length > 3 m). Canopy cover was measured using a concave densiometer at the center of the plot.

Within each plot I placed four 10-m transects in the cardinal directions emanating from the center of the plot. At point intervals of 2 m along the transects I placed a 7.6-m telescopic pole and counted the number and species of vegetation hits (Wiens and Rotenberry 1981) in each 1-m vertical layer. Thus the total number of points sampled with the pole in the plot was 21 (five points per cardinal transect and one center point). Pinnately compound leaves were counted as one hit each. The maximum number of *Tillandsia* hits per 1-m layer was 10 for simplicity (hits of other species could

exceed 10 per layer, but this rarely happened). Hits above 7.6 m were estimated after

obtaining the nest and tree heights, usually with a clinometer. At each of the 21 points I

measured the maximum canopy height within 10 cm of the pole, and the maximum of

these heights was the maximum height variable for the plot.

I divided the vertical profile into three strata to describe the ground layer (0-1 m),

shrub layer (1-3 m), and tree layer (>3 m). Pole hits were calculated into two primary

variables. Foliage frequency was defined as the sum of the points with foliage hits,

divided by the total number of points (21) on the plot. Foliage frequency was calculated

for the three vertical layers and also graphically represented for each 1-m layer. Foliage

density was defined as the number of foliage hits summed at all 21 points in each of the

three layers. To determine if *Tillandsia* species were more common at nest plots, I

summed the totals of *T. usneoides* and *T. recurvata* foliage hits in all vertical layers and

included this number as an overall measure of *Tillandsia* foliage density.

I used two indices of structural heterogeneity at the plot. I calculated the

variation in vegetation height across the plot using the heterogeneity index of Wiens and

Rotenberry (1981), where height variation = (maximum vegetation height – minimum

vegetation height)/mean vegetation height. A height-variation value of zero indicates a

uniform height across the plot, whereas a large value indicates more variation in the

height of the foliage on the plot. I calculated vertical structural diversity (VSD) among

the three vegetation layers using a Simpson diversity index (Hill 1973) following Braden

(1999): VSD = $1/\Sigma(p_i^2)$, where p_i is the proportion of foliage hits in vertical layer *i* on a

plot. A VSD near 1 indicates large variation in hits among the three layers, while a VSD

of 3 indicates no variation in hits among the three layers.

Floristic composition of paired plots. To compare which plant species were most commonly associated in the shrub and tree layers of nest plots and non-use plots, I summarized the pole-hit data using importance values derived in a similar manner to that of Lonard and Judd (2002). For each species I pooled hits from live and dead plant material. The density of a species was the total number of foliage hits at all nest plots or non-use plots. Frequency was defined as the proportion of plots at which a species was present. Relative frequency and relative density were summed to give the importance value for the species in the shrub and tree layers. Importance values thus describe how often a species occurs at plots and how much space the species occupies at the plot. For simplicity I present only the species with the five greatest importance values for each plot-type and layer. I calculated *Tillandsia* species separately from other species.

STATISTICAL ANALYSES

Nest success. I used the program CONTRAST (Hines and Sauer 1989) with a chi-square test to compare daily nest survival rates between incubation and nestling stages.

Nest-placement angles. I used Rayleigh's test (Zar 1996) to determine if the mean trunk-to-nest angle and the mean nest-opening angle described nonrandom distributions.

Nest-site selection. I used Matched-pairs Logistic Regression (MPLR) to explore habitat preferences for nest placement (Hosmer and Lemeshow 2000). I first calculated mean differences of nest-site variables between nest plots and non-use plots. To select variables for the multivariate MPLR, I entered each of the 15 nest-site variables into a

univariate MPLR and retained the variable if its Likelihood Ratio Test was significant at

$P < 0.25$, as recommended by Hosmer and Lemeshow (2000). I then checked for

collinearity among the selected variables and entered each correlated ($r > 0.6$; $P < 0.001$)

variable into separate multivariate analyses, following Beck and George (2000) and

Chase (2002). To obtain reduced MPLR models I used a backward elimination method,

starting with a full model and eliminating variables when they did not significantly

contribute to the model (Likelihood Ratio Tests, $P > 0.10$). I assessed goodness of fit by

using the residual analysis suggested by Hosmer and Lemeshow (2000). I compared the

final models using Akaike's Information Criterion for small samples (AIC_c) as

recommended by Burnham and Anderson (2002). The best model of the group was the

one with the smallest AIC_c. I present only those models with AIC differences (Δ_i) less

than 10.

   Nesting-outcome habitat differences. I used univariate binary logistic regression

with a likelihood ratio statistic to compare mean habitat variables between successful

and failed nests. Variable and model selection were performed in the same manner as

with the MPLR for nest-site selection. I used Rayleigh's test (Zar 1996) to test whether

the mean stem-to-nest angles and mean nest-opening angles of successful and failed

nests described nonrandom distributions. If angular distributions were nonrandom, I

compared mean stem-to-nest angles and mean nest-opening angles between successful

and depredated nests using a Watson-Williams test with an F ratio. I used a 2x2

contingency table with a Pearson chi-square test to compare nest types among nest trees

and to compare nest success and failure among the two primary nest types.

I used SPSS for Windows, versions 11.0 and 12.0 (SPSS 2001, 2003) for all statistical analyses except Rayleigh's test and daily survival rate differences. An alpha level of 0.05 was used for all tests unless noted otherwise. Means other than nesting stage lengths are presented as ± 1 SE.

RESULTS

I located 28 tyrannulet nests during 2002 and 2003 (Table 15). The percentages of nests found during the building, laying, incubation, and nestling stages were 64% ($n = 18$), 6% ($n = 1$), 21% ($n = 6$), and 7% ($n = 2$), respectively. One nest was found during either the incubation or nestling stage.

The first nests of each year were under construction by 1 April 2002 and 17 March 2003, and the latest active dates for known nests during each year were 30 August 2002 and 23 July 2003. A nest was also found at Santa Ana in early September 2004 (T. Brush, unpubl. data). The mean of the minimum observed building times rounded to the nearest whole day was 7 days ($n = 13$, range 2-15). Estimated mean lengths of the incubation and nestling stages were 14.0 days ($n = 8$, range $12 - 15.5$) and 18.5 days ($n = 9$, range $16 - 21$), respectively.

Behavior at the nest. Females, identified by their *pee-uk* call, were seen doing all nest-building, except one time when a male delivered a small twig to a nest immediately after his mate placed material in the nest. Several nests were located more easily when brooding females in the nest made trill contact calls to nearby singing males. I also noticed that males would often intersperse their *pier-pier-pier* songs with the trill call when there were no apparent females around, often in areas where I could not locate

Table 15. Number of Northern Beardless-Tyrannulet nests ($n = 28$) tended by estimated number of breeding pairs (determined by nearby re-nesting or simultaneously-active nests) at sites in the Lower Rio Grande Valley, Texas, 2002-2003. Suspected breeding pairs whose nests were not found are not included here.

Site	2002		2003	
	nests	breeding pairs	nests	breeding pairs
Anzalduas County Park	0	0	1	1
Bentsen	7	2	8	3
Gabrielson	1	1	3	1
Madero[a]	0	0	0	0
Santa Ana	5	2	3	2
Total	13	5	15	7

[a] I saw a nest being built at Madero in 2003 but it was abandoned 1-2 days later.

nests or females. I was able to see females brooding inside the nest at most nests that reached the incubation stage. On several occasions females were seen making the *pier-pier-pier* call near the nest, which is typically described as a male call in the literature (Brush 1999, Tenney 2000). When this vocalization was made by females, it was much softer than the typical call exhibited by males.

NESTING SUCCESS

Twelve (43%) of the 28 nesting attempts were successful and 16 (57%) failed. Of the failed nests, four (25%) failed during incubation, seven (44%) failed during the nestling stage, and 1 failed during either the incubation or nestling stages. Four (25%) of the failed nests appeared completely built but were abandoned before incubation began. Because of the inaccessibility of these nests, I could not be certain that eggs were never laid, and I included them in the analysis. Although the incubation daily survival rate appeared slightly greater than the nestling-stage daily survival rate, the two rates were not significantly different ($\chi^2_1 = 0.6$, $P = 0.4$; Table 16).

Nestlings could be heard softly begging ('*bee-bee*' call; Tenney 2000) from the nests as early as 11 to 12 days of age, and could sometimes be seen from a distance with binoculars at this point. Older nestlings often begged loudly from the nest and their heads sometimes protruded from the nest entrance when adults arrived with food. The mean number of fledglings for successful nests was 2.1 ± 0.2 ($n = 9$, range 1-3), but this could have been an underestimate, because fledglings could have gone undetected. The maximum number of successful broods from what appeared to be the same nesting pair was two, and the maximum number of nesting attempts was four. On two occasions I

Table 16. Mayfield daily survival rates for Northern Beardless-Tyrannulet nests during incubation (INC), nestling (NSTL), and incubation and nestling (Overall) in the Lower Rio Grande Valley, Texas, 2002-2003.

Nest stage	Daily nest survival	SE	n	Exposure days	Losses	Nest success (%)[a]
INC	0.983	0.008	21	233.5	4	78.5
NSTL	0.973	0.010	19	263	7	60.7
Overall	0.978	0.007	23	496.5	11	48.3

[a] Nest success $_{INC}$ = (Daily nest survival $_{INC}$)^{14}; Nest success $_{NSTL}$ = (Daily nest survival $_{NSTL}$)$^{18.5}$; Nest success $_{Overall}$ = (Daily nest survival $_{Overall}$)$^{32.5}$.

observed females re-building 1-2 days after a single chick had fledged from a nearby nest and was still being fed in the area.

CAUSES OF NEST FAILURE

Because few of the 16 failed nests could be closely inspected, causes of failure were difficult to ascertain. Six nests appeared to be ripped open or ripped down, likely by a predator. Of these nests, four had nestlings, one had eggs, and the sixth had either eggs or young chicks. Only once did I see a potential predator near a nest that caused distress to the adult tyrannulets. Two juvenile Cooper's Hawks (*Accipiter cooperii*) that had probably fledged from a nest about 0.7 km away were perched near a tyrannulet nest in 2003 at Bentsen, apparently interested in the tyrannulet breeding pair that had been delivering food to the nest. The tyrannulets appeared agitated and were making a monotonous downslurred '*peeeeu*' distress call. The Cooper's Hawks eventually noticed me watching and flew away. The nest later fledged at least two young. A tyrannulet nest at Santa Ana depredated during the nestling stage was about 50 m from a Harris's Hawk nest.

Six failed nests appeared intact but could not be closely inspected. Three of these failed during possible egg-laying, one failed during incubation, and two failed during the nestling stage. Of the two nests that apparently failed from severe weather, one failed during a severe storm with golf-ball sized hail during incubation. The other nest appeared to be partially disintegrated after a heavy thunderstorm during the previous night, also during incubation.

A nest at Anzalduas County Park was found to have been depredated after a

large, dead cedar elm about 20m away had been cut down since our previous visit. The nest had a small hole in its underside, and it is unclear if felling the nearby tree affected the outcome of the nest.

NEST-PLACEMENT AND NEST-SITE CHARACTERISTICS

Tyrannulets in this study were attracted to areas rich in *Tillandsia* and with tall trees, nesting almost exclusively in cedar elm. Ninety-three percent (26 of 28) of nests were built in cedar elm, 11 of which were dead. The two other nests were built in Texas ebony. The Texas ebonies at Bentsen used for nesting were relatively small compared to some large, moss-laden ebonies at Santa Ana, and tyrannulets may prefer the more open canopy structure of cedar elm. Mean nest height was 9.1 ± 0.4 m (range 4.9-14.0), mean nest tree height was 13.0 ± 0.5 m (range 8.5-18.0), mean nest tree dbh was 37.1 ± 2.8 cm (range 20.8-74.3), and mean horizontal distance from the nest to the nest-tree trunk was 3.5 ± 0.4 m (range 0.3-7.9).

All active tyrannulet nests were built in or on *Tillandsia* epiphytes, although in 2003 I saw a female apparently attempting to build a nest (which was never completed) in a clump of dead leaves and either spider webs or caterpillar webs in a mulberry (*Morus* sp.) sapling at Madero. I noticed two general types of nests: (1) those built inside Spanish moss clumps that were often suspended from branches; and (2) nests that were built among ball moss clumps, appearing to have a more stationary base such as a branch or a ball moss clump. However, even nests primarily built in ball moss nearly always had a large amount of Spanish moss incorporated into the nest walls. Fifty seven percent (16 of 28) of the nests were of the ball-moss type, and 43% (12 of 28) of the

nests were of the Spanish-moss type. Of the Spanish-moss nests, 92% (11 of 12) were located at Bentsen. Distribution of the nest types among the nest-tree type was as follows: 11 ball moss nests and four Spanish moss nests in live cedar elm; five ball moss nests and six Spanish moss nests in dead cedar elm: two Spanish moss nests in Texas ebony. Distribution of nest types among live cedar elm and dead cedar elm was not significantly different than expected (Pearson $\chi^2_1 = 2.1$, $P = 0.15$). Mean stem-to-nest angle, $\bar{a}$, was 271 degrees, but the distribution was random ($z = 2.8$, $0.10 > P > 0.05$). Distribution of the nest-opening angles was also random ($\bar{a} = 276$ degrees; $z = 1.5$, $P > 0.2$).

Nest plots on average had a lower foliage frequency in the 1-7 m strata than non-use plots, and nest plots generally had taller vegetation than non-use plots (Figure 10). Five of the 15 nest-site MPLR variables were significant in univariate analyses (Table 17). Height variation was correlated with canopy cover (Spearman $r_s = -0.72$, $P < 0.001$) and shrub-layer foliage frequency ($r_s = -0.63$, $P < 0.001$), and was therefore separated from these variables in the multivariate analysis. The best final MPLR model contained only one variable and indicated that the total amount of *Tillandsia* foliage hits best predicted nest-site selection (Table 18). The *Tillandsia* MPLR model had nearly five times the predictive power of the next best model, which included canopy cover and maximum vegetation height. The residual analysis indicated that all three models fit the data well.

Proportions of Spanish moss and ball moss were the same on nest plots and non-use plots (Pearson $\chi^2_1 = 3.8$, $P = 0.052$), with Spanish moss accounting for 90-93% of
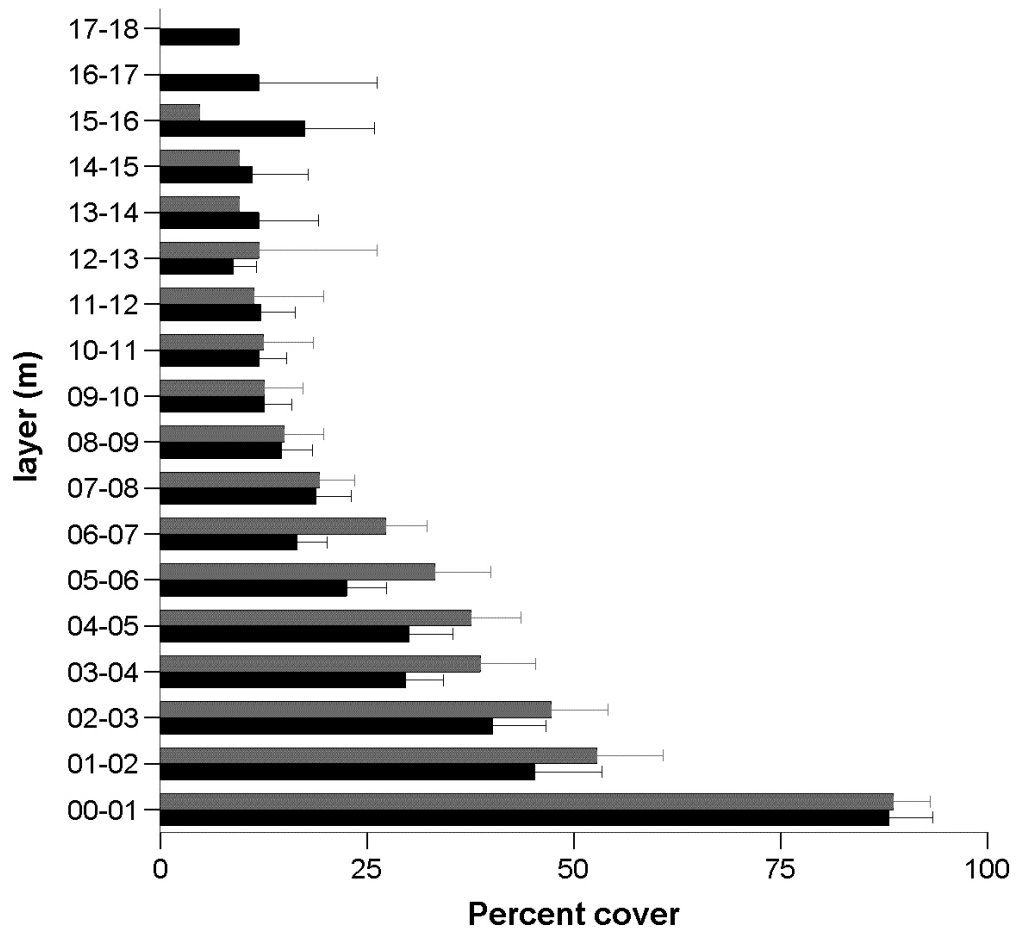
Figure 10. Foliage frequency for each vertical meter layer obtained from vegetation hits on a vertical pole placed at 21 points within nest plots (*n* = 28; black bars) and non-use plots (*n* = 28; gray bars) for Northern Beardless-Tyrannulet nests in the Lower Rio Grande Valley, Texas, 2002-2003. Error bars represent 2 SE.

Table 17. Summary of mean differences of nest-site variables between paired nest plots and non-use plots for Northern Beardless-Tyrannulet nests ($n = 28$) in the Lower Rio Grande Valley, Texas, 2002-2003. Likelihood Ratio Test statistic (LRS χ^2_1) and P values are from univariate 1-1 matched pairs logistic regression (MPLR). Asterisks denote significance for inclusion in the multivariate MPLR ($P < 0.25$).

Variable	$\bar{x}$ difference	SE	LRS χ^2_1	P	Correlations[a]
% canopy cover	-8.9	5.1	3.0	0.09*	A
Large trees (15-30 cm dbh)	0.1	0.3	0.0	0.8	
Small trees (>30 cm dbh)	-0.8	0.8	1.0	0.3	
Snags	0.5	0.6	0.6	0.4	
Logs	0.5	0.6	0.6	0.5	
Maximum height	2.7	0.5	21.0	<0.001*	
Height variation	0.3	0.2	3.6	0.06*	AB
Foliage frequency, 0-1 m (%)	-0.6	2.6	0.0	0.8	
Foliage frequency, 1-3 m (%)	-7.8	3.2	5.6	0.02*	B
Foliage frequency, > 3 m (%)	-3.9	4.9	0.6	0.4	
Foliage density, 0-1 m	10.1	7.3	2.0	0.16*	
Foliage density, 1-3 m	-7.7	10.8	0.5	0.5	
Foliage density, >3 m	11.4	13.3	0.8	0.4	
Vert. structural div. (VSD)	0.0	0.1	0.1	0.8	
Total *Tillandsia* hits	61.5	11.2	27.7	<0.001*	

[a] Matching letters indicate variables that were significantly correlated (Spearman Rank Correlation; $|r_s| \geq 0.60$, $P < 0.001$) and thus were not included in the same multivariate model.

Table 18. Final MPLR models describing nest-site selection for Northern Beardless-Tyrannulet nests ($n = 28$) in the Lower Rio Grande Valley, Texas, 2002-2003. LRS = Likelihood Ratio χ^2 Statistic; K = number of parameters; AIC$_c$ = Akaike Information Criterion; Δ_i = AIC differences; w_i = Akaike weights.

Model # and Variable(s)	Coefficient	SE	LRS[ab]	K	AIC$_c$	Δ_i	w_i
1			27.7 **	2	15.6	0.0	0.805
Tillandsia foliage density	0.095	0.043	27.7 **				
2			27.1 **	3	18.8	3.2	0.167
canopy cover	-0.087	0.052	6.0 *				
max. height	1.100	0.462	24.1 **				
3			21.0 **	2	22.3	6.7	0.029
max. height	0.919	0.338	21.0 **				

[a] The LRS of the full model vs. null model is shown on the first row for each model, and the LRS for the full model versus the model without the variable is shown next to each variable. For univariate models 1 and 3, both LRS tests described above are the same.
[b] *$P < 0.05$; **$P < 0.001$

the *Tillandsia* hits on each plot type. Nest plots had about six times the amount of

Spanish moss as non-use plots (1843 vs. 303 hits), and ball moss hits on nest plots were

about 10 times as abundant as on non-use plots (202 vs. 21 hits). A finer-scale

comparison showed that *Tillandsia* foliage density was greater in all three foliage strata

on nest plots than on non-use plots (Figure 11).

Nesting areas had abundant thorny vegetation (e.g., Wright acacia, granjeno,

brasil, colima), like the available habitat (Table 19). Most of the *Tillandsia* hits on the

plots were from Spanish moss (Table 20). Non-use plots had much more mesquite

foliage, which rarely serves as a substrate for *Tillandsia* growth (personal observation).

Although nesting areas tended to have tall trees with abundant Tillandsia, most

tyrannulets seemed to be flexible in their foraging habits. I often saw birds forage in

scrubby areas when they were away from the nest, although they frequently foraged in

the forests as well.

HABITAT DIFFERENCES AT SUCCESSFUL VS. FAILED NESTS

Nesting outcome appeared to be random with respect to nests placed in dead cedar elm

versus live cedar elm, and neither of the two nests in Texas Ebony were successful

(Figure 12). Among the nest-placement variables and nest-site variables at successful

and failed nests, only the number of small trees was significantly different for inclusion

in any multivariate binary logistic model (LRS $\chi^2_1 = 2.2$, $P = 0.14$), but this variable did

not meet the final α criteria of 0.10 to be considered different (Table 18). The

percentages of successful nests in ball moss (44%: seven of 16) and in Spanish moss

(42%: five of 12) were not statistically different (Pearson $\chi^2_1 = 0.01$, $P = 0.9$).

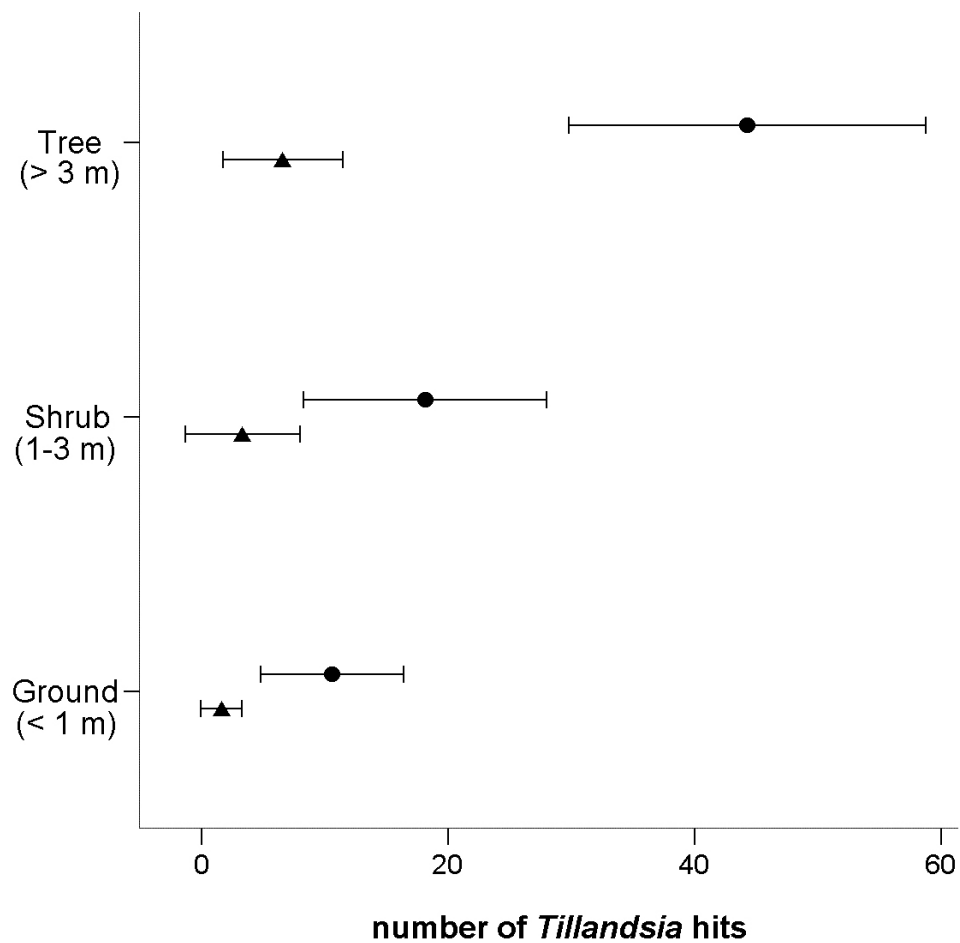Figure 11. Differences in total *Tillandsia* hits at nest plots (circles) and non-use plots (triangles) among three strata for Northern Beardless-Tyrannulet nests in the Lower Rio Grande Valley, Texas, 2002-2003. Nest plots had more *Tillandsia* in all three layers (Mann-Whitney *U*-tests: Ground, $U = 226.5$, $P < 0.01$; Shrub, $U = 198$, $P < 0.001$; Tree, $U = 72$, $P < 0.001$). Error bars represent 2 SE.

Table 19. Species with the five greatest importance values, not including *Tillandsia* epiphytes, determined by foliage hits in the shrub and tree layers at Northern Beardless-Tyrannulet nest plots (*n* = 28) and non-use plots (*n* = 28) in the Lower Rio Grande Valley, Texas, 2002-2003. D = density, or total number of foliage hits; RD = relative density (%); F = frequency of plots that had foliage hits of the species (%); RF = relative frequency (%); IV = importance value.

Species	Common name	D	RD	F	RF	IV
Tree layer (>3 m)						
Nest plots						
Ulmus crassifolia	cedar elm	878	35.3	92.9	17.9	53.2
Acacia greggii	Wright acacia	263	10.6	50.0	9.7	20.2
Condalia hookeri	brasil	190	7.%	46.4	9.0	16.6
Celtis laevigata	sugar hackberry	205	8.2	32.1	6.2	14.4
Cocculus diversifolius	snail seed	87	3.5	53.6	10.3	13.8
Non-use plots						
Prosopis glandulosa	mesquite	638	19.8	57.1	9.1	28.9
Celtis pallida	granjeno	328	10.2	71.4	11.4	21.6
Ulmus crassifolia	cedar elm	419	13.0	50.0	8.0	21.0
Condalia hookeri	brasil	267	8.3	57.1	9.1	17.4
Acacia greggii	Wright acacia	290	9.0	46.4	7.4	16.4
Shrub layer (1-3 m)						
Nest plots						
Celtis pallida	granjeno	508	21.8	89.3	11.7	33.5
Condalia hookeri	brasil	272	11.7	50.0	6.5	18.2
Zanthoxylum fagara	colima	160	6.9	57.1	7.5	14.4
Cocculus diversifolius	snail seed	121	5.2	57.1	7.5	12.7
Diospyros texana	Texas persimmon	161	6.9	39.3	5.1	12.1
Non-use plots						
Celtis pallida	granjeno	776	26.1	85.7	10.2	36.3
Condalia hookeri	brasil	343	11.5	71.4	8.5	20.1
Sideroxylon celastrinum	la coma	175	5.9	53.6	6.4	12.3
Ziziphus obtusifolia	lotebush	193	6.5	46.4	5.5	12.0
Phaulothamnus spinescens	snake eyes	205	6.9	32.1	3.8	10.7

Table 20. Importance values of *Tillandsia* epiphytes, determined by foliage hits in the shrub and tree layers at Northern Beardless-Tyrannulet nest plots (*n* = 28) and non-use plots (*n* = 28) in the Lower Rio Grande Valley, Texas, 2002-2003. D = density, or total number of foliage hits; RD = relative density (%); F = frequency of plots that had foliage hits of the species (%); RF = relative frequency (%); IV = importance value.

| Species	Common name	A	RA	F	RF	IV
Tree layer (>3 m)						
Nest plots						
Tillandsia usneoides	Spanish moss	1055	85.1	89.3	59.5	144.6
Tillandsia recurvata	ball moss	185	14.9	60.7	40.5	55.4
Non-use plots						
Tillandsia usneoides	Spanish moss	164	88.6	35.7	76.9	165.6
Tillandsia recurvata	ball moss	21	11.4	10.7	23.1	34.4
Shrub layer (1-3 m)						
Nest plots						
Tillandsia usneoides	Spanish moss	501	98.6	67.9	90.5	189.1
Tillandsia recurvata	ball moss	7	1.4	7.1	9.5	10.9
Non-use plots						
Tillandsia usneoides	Spanish moss	93	100.0	25.0	100.0	200.0
Tillandsia recurvata	ball moss	0	0	0	0	0
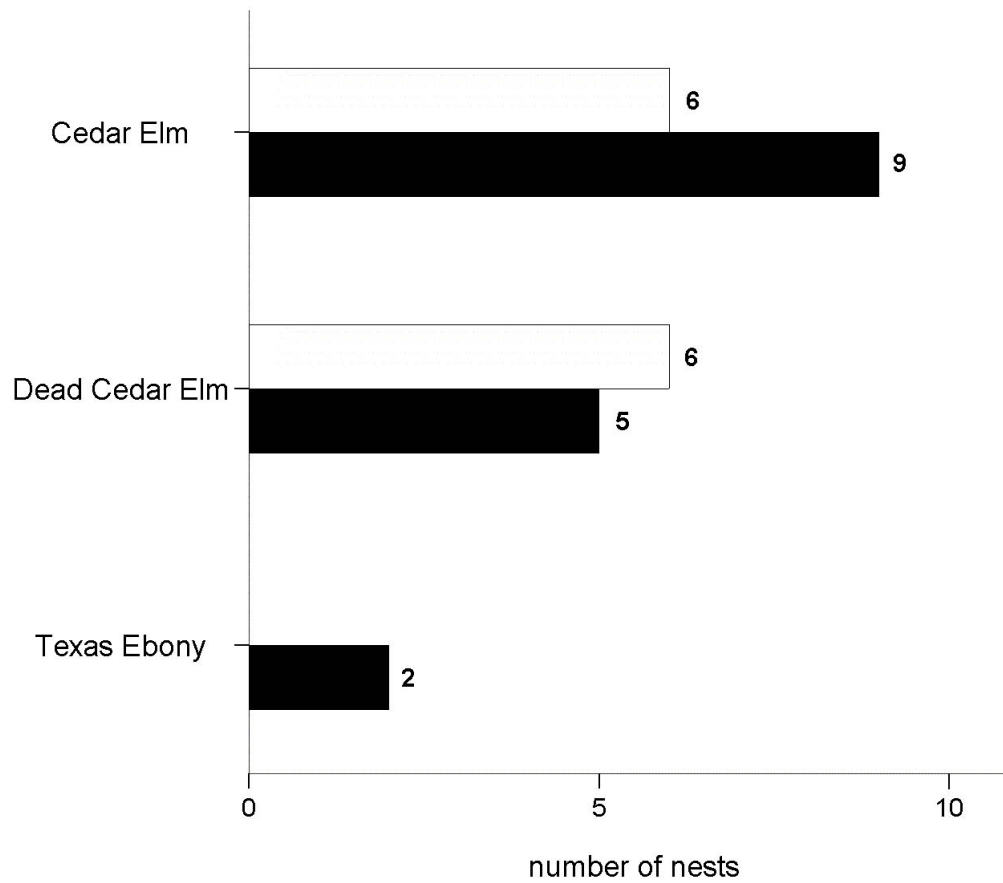
Figure 12. Nest trees and outcome for Northern Beardless-Tyrannulets during 2002-2003 (*n* = 28). White bars represent successful attempts and dark bars indicate failed attempts.

There was a slight association between the nest's condition when failing and the nest stage at failure. At least four of the six nests that appeared ripped apart had been in the nestling stage, while only two of the six nests that appeared intact failed with nestlings in them, suggesting a difference in predator or predation mechanism during the two stages.

NEST DISTRIBUTION AT THE STUDY SITES

Bentsen. I estimated that there were at least three territories and possibly as many as five at Bentsen (two areas appeared to be occupied by lone singing males). There were two territories during each year that accounted for most of the nests found. These were located in two forested areas in the northern portion of the park (Figure 13). One territory at the southern end of the Singing Chaparral Trail (SCT) was in a thorn-forest area with many live and dead cedar elms with abundant Spanish moss and shorter brasils, Texas ebonies and Wright Acacias. This terrace bordered a small bottomland area with cedar elms and sugar hackberries, beyond the southern end of the SCT. A small resaca, called the "water hole" on park maps, was dry during this study. Tyrannulets during both years built all their nests in the thorn forest, although I surmised that an unfound nest was located in the bottomland area because of the delivery of nesting material to that area (this undiscovered nest probably failed because of soon re-nesting thereafter).

The second territory was in and to the east of the trailer loop, which was a mixture of thorn scrub and thorn forest. Tall cedar elms and mesquites were scattered in a dense shrub-layer with several roads, campsites, and picnic areas. Three of the 2003

Table 18. Habitat variables associated with successful (n = 12) and failed (n = 16) Northern Beardless-Tyrannulet nests in the Lower Rio Grande Valley, Texas, 2002-2003. None of the variables were significantly different in the logistic regression (Likelihood Ratio Statistic, P < 0.05).

	Successful			Failed	
Variables	$\bar{x}$	SE		$\bar{x}$	SE
Nest-placement variables					
Nest height (m)	8.8	0.7		9.3	0.5
Nest tree height (m)	12.9	0.8		13.1	0.7
Nest tree dbh (cm)	39.7	4.5		35.2	3.6
Stem to nest distance (m)	3.6	0.6		3.3	0.5
$\bar{a}$, stem to nest (°)[a]	239	-		280*	-
$\bar{a}$, nest opening (°)[a]	195	-		295	-
Nest-site variables					
% canopy cover	52.6	6.8		55.5	4.7
Large trees, 15-30 cm dbh	1.8	0.4		1.6	0.3
Small trees, >30 cm dbh	3.1	0.8		5.3	1.1
Snags	2.3	0.7		2.3	0.6
Logs	2.7	0.6		3.4	0.8
Max. veg. height	12.4	0.8		12.4	0.6
Height variation	2.1	0.3		2.1	0.1
Foliage frequency, 0-1 m (%)	90.9	2.6		86.0	4.3
Foliage frequency, 1-3 m (%)	56.7	7.7		58.0	5.8
Foliage frequency, > 3 m (%)	68.7	7.4		65.8	4.7
Foliage density, 0-1 m	139.5	9.9		136.0	11.2
Foliage density, 1-3 m	101.3	15.7		103.3	14.4
Foliage density, >3 m	136.4	27.5		131.1	13.6
Vert. structural div. (VSD)	2.5	0.2		2.6	0.1
Total *Tillandsia* hits	77.2	20.6		69.9	19.0

[a] Mean angles, $\bar{a}$, with asterisk represents a significant nonrandom circular distribution (Rayleigh's test, P < 0.05; Zar 1996). Non-significant mean angles are uninformative because the circular distributions are random.
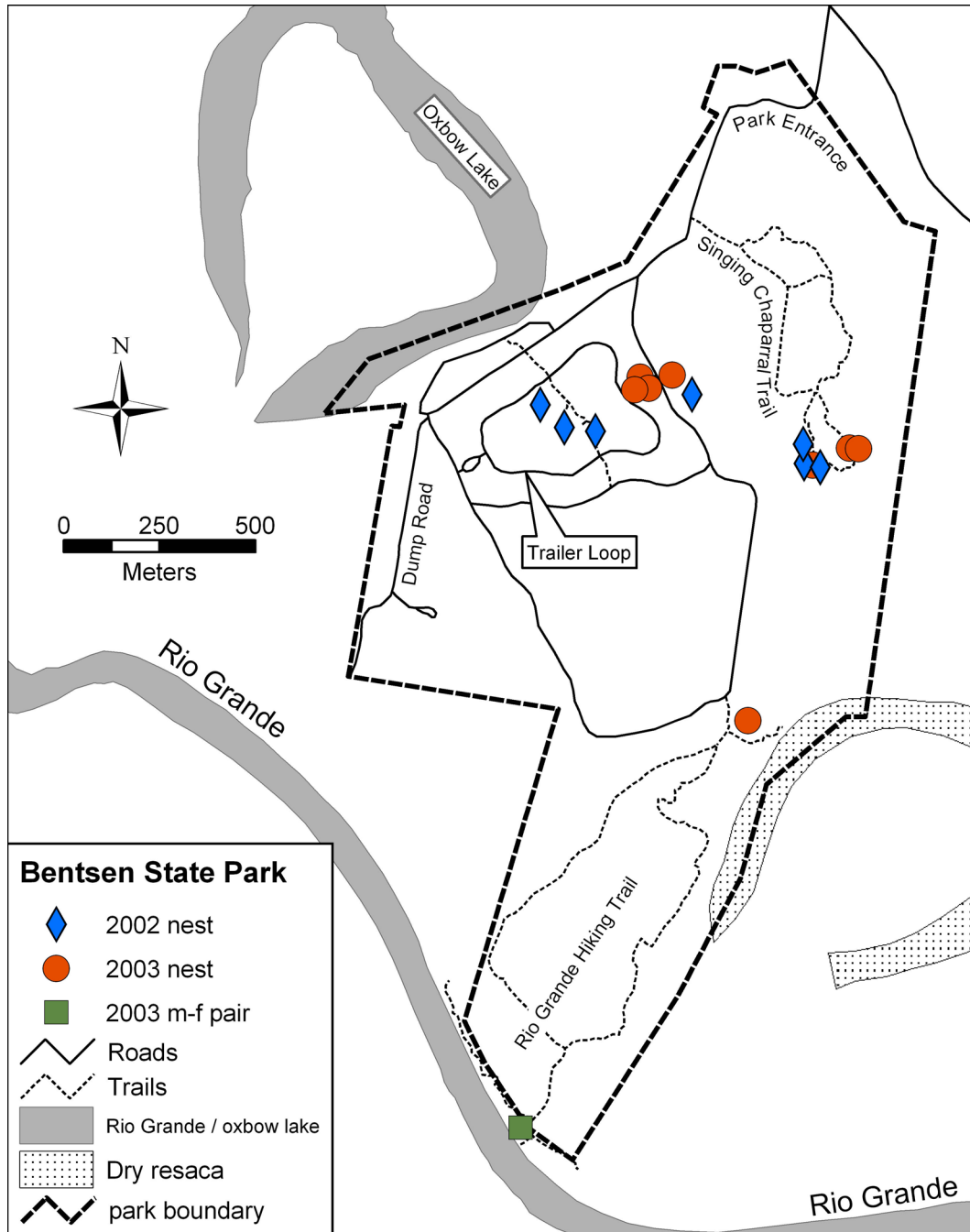
Figure 13. Locations of Northern Beardless-Tyrannulet nests and male-female pair at Bentsen-Rio Grande Valley State Park, 2001-2003.

nests were built within about 10 m of one another. One nest in 2003 was located in a small, densely-forested area with tall trees just east of the eastern trailer loop entrance.

I apparently found a third and possibly fourth breeding pair with a nest located at the Rio Grande River Hiking Trail (RGRHT) trailhead and a pair of tyrannulets near the Rio Grande, about 1.2 km from that nest. The trailhead area was near a large resaca and formerly supported tall forest but experienced a wildfire in 1999 and had few cedar elms or *Tillandsia* in 2003. I also regularly observed a singing male near the dump road in 2003 and a singing male near the park entrance during both years.

Santa Ana. Fewer nests were found at Santa Ana and the number of territories was difficult to estimate. There were probably four or five territories here, but there could have been more than five because Santa Ana was not as thoroughly searched as Bentsen. (Figure 14). I found nests here in three areas: Willow Lakes; Cattail Lakes; and off the Jaguarundi trail. Willow Lakes has thorn-forest and bottomland characteristics because of active water management by the refuge. The tyrannulet nests at Cattail Lakes were in thorn forest but there was extensive bottomland-type forest just south of the tour loop road that the nesting pairs used for foraging. In the Jaguaraundi/Owl/Resaca area I regularly heard tyrannulets but found only one nest. In July 2001 I located a male-female tyrannulet pair in the flooded forest off the Owl Trail, and the male chased away a Couch's Kingbird, suggesting that there may have been a nest in the vicinity. A family group with at least two fledglings was found east of the Vireo trailhead in July 2001. There is extensive thorn forest and bottomland forest throughout this southern portion of the refuge, and territories were difficult to discern.
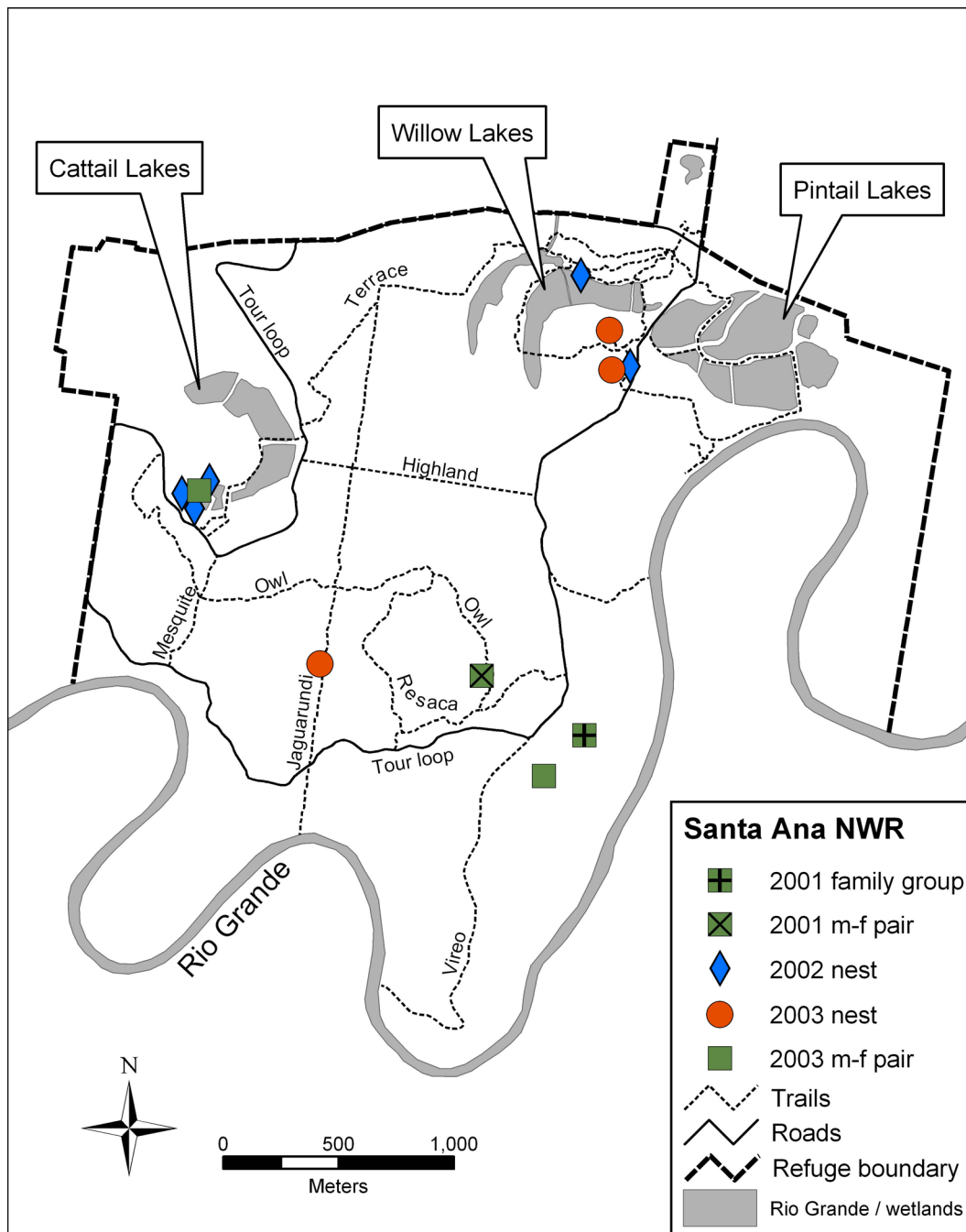
Figure 14. Locations of Northern Beardless-Tyrannulet nests, male-female pairs, and family group at Santa Ana National Wildlife Refuge, 2001-2003.

The north-central area (Highland trail) of Santa Ana is primarily chaparral, which does not support *Tillandsia*, but there are many areas of tall thorn forest near the Rio Grande, southeast and southwest of Pintail Lakes that were not searched adequately for tyrannulets.

Madero, Gabrielson, and Anzalduas County Park. These sites contained areas with tall thorn forest and bottomland forest, likely because of high water tables created by Anzalduas dam. There were at least three territories at these three sites combined during 2003. Nests at Gabrielson were all found along a resaca with bottomland and thorn forest in the northwestern portion of the tract. There was extensive thorn forest in central Gabrielson, but most of it was not surveyed. Much of Anzalduas County Park was covered by tall forest with abundant Spanish Moss, but the understory had been cleared for picnic grounds. The territory covered by the pair at the 2003 Anzalduas nest probably included the park due north in Mexico, across the Rio Grande, and possibly southern Madero.

Singing tyrannulets at Madero were usually found along the western periphery and at the entrance (northeast corner), which are areas with large sugar hackberries and cedar elms but only small amounts of *Tillandsia*. A bottomland forest along the southern edge of Madero grades into thorn forest, but access was difficult here and the area was not thoroughly searched. The canal along the eastern edge of the tract appears to provide moisture for different-sized patches of trees along its entire length.

DISCUSSION

INCUBATION AND NESTLING DEVELOPMENT PERIODS

My estimate of 14 days for incubation is within the 14-16 day range that Skutch (1997) cited for the Southern Beardless-Tyrannulet (*Camptostoma obsoletum*), which was formerly thought to be conspecific with the Northern Beardless-Tyrannulet (Stiles and Skutch 1989). Other birds in the Elaeniinae subfamily listed by Skutch have nestling periods similarly as long (up to 21 days) as the tyrannulet. These nesting periods are considerably longer than many temperate open-cup-nesting Tyrannids and other passerines (Ehrlich et al. 1988) and probably result in stronger fledglings that require less parental vigilance after they have left the nest. I noticed that many tyrannulet fledglings were quite capable of flight as soon as they left the nest. They appeared much more mobile than fledglings of other passerine species at the study sites.

The somewhat small clutch size of one to three eggs inferred from the number of fledglings and from Tenney's (2000) review is typical of tropical species that have likely adapted to greater levels of nest predation in the tropics compared to temperate zones (Stiles and Skutch 1989). Smaller clutches are not as noticeable to predators as large clutches and represent a lower energetic output that can be replaced more easily if the nest is lost. The long nesting season of March to September found in this study, which was also observed by Brush (1999), allows tyrannulets to re-nest after multiple failures and raise multiple broods.

Further study is needed into the vocalizations of males and females and their meaning within a breeding context. Brush (1999) and Tenney (2000) suggested that trill

calls are likely a kind of contact call exchanged between a nesting pair. Males that are searching for a female or a new territory probably intersperse the *pier-pier-pier* song with trills calls to elicit a response of a potential mate, as I saw in certain areas where no nests or females could be found. Studies of marked birds could establish whether only females give the *pee-uk* call, although I was fairly sure that this call was only given by individuals that incubated in the nest, which is assumed to be the female (Brush 1999, Tenney 2000).

NESTING SUCCESS AND NEST-SITE CHARACTERISTICS

Brush's (1999) study is the only one I am aware of that presents nest success results of multiple Northern Beardless-Tyrannulet nests. Six of his 11 nests likely fledged, three nests were abandoned or depredated, and two nests' outcomes were unknown. His 55% (six of 11) raw success rate is slightly larger than the 43% I observed.

My sample sizes for daily survival rates (21 nests during incubation; 19 nests during the nestling stage) were around the bare minimum of 20 recommended by Hensler and Nichols (1981) for estimating survival rates. Further study with larger samples is needed to get more robust survival rate estimates and to relate these to habitat parameters. Future researchers should delineate territories and make more extensive measurements of the habitat, rather than focusing exclusively on the nest habitat.

I was able to determine that tyrannulets build their nests in areas with more *Tillandsia* than the nearby habitat. However, tyrannulets in this region may not be strictly dependent upon *Tillandsia* for nest placement, as was suggested by the observation of nest-building in dead leaves and webbing. The area of Madero where this

behavior was seen has abundant sugar hackberry, huisache, and granjeno but little cedar elm and virtually no *Tillandsia*. In Arizona, tyrannulets build nests on the dense webs of tent caterpillars (Lasiocampidae), spider webs, or in mistletoe (Phillips et al. 1964). My observation at Madero was similar to that described in Sabino Canyon, Arizona, by Brandt (1951:151), with the bird placing small bits of dead leaf material in webbing. Tyrannulets have been observed along the Rio Grande near the town of La Joya, approximately 12 km west-northwest of Bentsen where there is little if any *Tillandsia* (S. M. Werner, unpubl. data; T. Brush, unpubl. data). Future work should include tyrannulet nesting surveys at sites that have much less *Tillandsia*, such as Madero, to determine whether tyrannulets in the LRGV really need *Tillandsia* as a nesting substrate.

Causes of nest failure. I did not detect any differences in the habitat parameters between successful and unsuccessful nests. Perhaps the structure of the nests could be just as important, or more important, as the surrounding habitat in affecting a nest's outcome. For instance, some tyrannulets may build sturdy nests that are less prone to the hazards of extreme weather events. I assumed that several nests failed from storm events (e.g., the hail storm), but I did not look specifically at nests that *survived* the effects of storms. Future investigations should look at tyrannulet nest designs and their susceptibilities to, and strengths against, storms and predators.

Raptors, such as the Cooper's Hawks observed at one of the Bentsen nests, may be one of the few predators that can depredate some of the nests built in hanging Spanish moss. Snakes and other non-flying vertebrates may be less able to closely approach a dangling nest. But the sturdier, ball moss-type nests are probably susceptible to many

predators. Skutch (1997) reported predation of two eggs by a snake at a Southern Beardless-Tyrannulet nest, although he did not describe the position of the nest. Eastern Fox Squirrels were seen regularly at the LRGV study sites, and other small rodent species such as those identified by Sternberg (2001) could be nest predators. Larger potential predators at the study sites include Gray Hawks, Harris's Hawks, White-tailed Hawks, Great Horned Owls, Great-tailed Grackles, and possibly opossums. Green Jays are common at the sites, but there is little evidence that they are nest-robbers, unlike other common North American jays such as Western Scrub-Jays and Blue Jays (Gayou 1995). Predators such as owls that hunt using audio cues might be able to key in on tyrannulet nests containing loud nestlings during the early morning or evening hours. It is nearly impossible to identify nest predators based on the condition of the nest (Lariviere 1999), but 24-hour monitoring cameras could be used to answer questions about tyrannulet nest predation and other failure events (e.g., Thompson et al. 1999, Renfrew and Ribic 2003). Recently, Thompson and Burhans (2003) used infrared cameras to record nest activity at night.

CURRENT AND FUTURE NESTING STATUS IN THE LOWER RIO GRANDE VALLEY

Northern Beardless-Tyrannulets are present on five of the largest parcels of mature native thorn forest in the LRGV, and probably breed on all five of these parcels. Nearly all of the breeding pairs during each year fledged young, and although only one nest at Santa Ana was successful, additional nests likely went undiscovered at this large tract. Certain areas at the sites appeared to be consistently occupied from 2001 to 2003,

suggesting no immediate changes in the population.   Current status compared to historical trends is nearly impossible to ascertain given the absence of historical nesting information available.

Bentsen. The only previously published records of tyrannulet nests at Bentsen are those of Brush (1999). He estimated three territories, roughly corresponding to the Singing Chaparral Trail, Trailer loop, and Rio Grande River Hiking Trail. I found territories in the same areas. Bentsen has distinct pockets of thorn forest and bottomland forest surrounded by drier areas of thorn scrub where mesquite is the dominant tree and *Tillandsia* is basically absent. Without some sort of flooding or a few years with above-normal rainfall, most of the forested areas will likely continue to degrade into habitat unfavorable to tyrannulets. The singing chaparral trail area has lost many large trees since Brush's (1999) study there (T. Brush, University of Texas – Pan American, personal communication). Large cedar elms in the central trailer loop area continue to die and fall down, and this area, which was once a dense forest, has become a scattered woodland. A large, dead cedar elm that supported a tyrannulet nest there in 2002 had mostly fallen down by spring 2003. Tyrannulets could benefit from larger trees that may grow from periodic flooding of the large resaca on the southeastern edge of Bentsen.

Santa Ana. Davis' (1940) breeding bird census, which was likely conducted near the Owl and Resaca trails at Santa Ana (see Cantu 1996) detected one tyrannulet nest. Castillo (1996) censused avian communities from October 1995 to September 1996 near the Owl and Resaca trails but did not detect any Northern Beardless-Tyrannulets. However, I found a suspected nesting pair in 2001 and a nest in 2003, both within about

100 m of two of his transects. Two other studies by Gehlbach (1987) during 1973-1978 and Cantu (1996) during 1995-1996 replicated on the same study plots near Willow Lakes at Santa Ana recorded no tyrannulet territories. But one of the 2002 tyrannulet nests found in the current study was located on one of these study plots, and two 2003 nests were located about 25 m and 115 m off the plots.

Santa Ana is the largest (853 ha) tract of native brush in this part of the LRGV and will likely remain a stronghold of tyrannulets into the future. Although it faces some of the same water-loss issues as Bentsen, it has large stands of thorn forest and bottomland forest compared to the small patches at Bentsen, probably only partly due to an active flooding program. There seems to be an abundance of tall trees rich with *Tillandsia*, especially in the southern and eastern portions of the refuge. I was unable to cover most of these areas thoroughly. Future efforts should be made to find all the tyrannulet territories at Santa Ana and attempt to delineate them with respect to habitat.

Gabrielson, Madero, Anzalduas County Park. Anzalduas County Park and the adjacent northwestern section of Gabrielson have a very lush tree layer that has many potential nest sites for tyrannulets. Because of Anzalduas Dam, this area probably does not need water management as urgently as Bentsen, but vegetation monitoring would probably be useful in exploring the dam's effect on plant communities. Gabrielson is closed to the public, but Anzalduas is a popular park for picnics and parties. As long as the dense tree canopy remains intact, weekend crowds might not adversely affect tyrannulets. A further concern is the new U.S.-Mexico bridge that will be built on the east side of Gabrielson, which will increase air pollution in the short-term and increase

local development in nearby Hidalgo and Mission over the long term.

FUTURE RESEARCH NEEDS

Much as Brush's (1999) study served as a pretext to my work, future studies of tyrannulets at these sites should be able to draw from my results and provide more information about these birds. Because tyrannulets and their nests are cryptic, future monitoring efforts will need to rely on keying in on the distinctive vocalizations exhibited by males and females. Tyrannulets at these sites also cover large areas, often traveling several hundred meters in a short time span, making monitoring difficult. Color-banding studies would provide much-needed data on territory sizes, overwintering habits, pair bonds, and yearly survivorship. Following marked individuals could also provide data on vocalizations, and yearly productivity. High-technology monitoring cameras would be helpful to investigate nesting behavior, nest predation, and nest loss and survival from severe weather events. In addition, the predator communities should be identified.

Efforts should be made to determine if tyrannulets are limited to areas in the LRGV with *Tillandsia* or if they are simply more common at those sites. The long-term viability of *Tillandsia* at these brush tracts should also be researched. Some populations of the Northern Parula (*Parula Americana*), which relies heavily on *Tillandsia* and other epiphytic species for nesting, have been extirpated from areas where high levels of air pollution have adversely affected epiphytic growth (Moldenhauer and Regelski 1996). As LRGV border cities continue to grow, air pollution could have negative effects on *Tillandsia*, as well as other flora and fauna of the native brush tracts.

HABITAT RESTORATION

Most of the remnant mature riparian and thorn forest in the LRGV has been preserved (Jahrsdoerfer and Leslie 1988), so future restoration efforts should focus on the re-planting of areas along resacas or other riparian/wetland formations to allow large trees to grow and persist. Some Lower Rio Grande Valley National Wildlife Refuge tracts near water sources are regenerating but are still absent of *Tillandsia* (e.g., Pharr Settling Basin), and every effort should be made to restore forests with *Tillandsia* epiphytes where possible. Increasing the availability of this habitat feature would probably benefit tyrannulet populations as well as other LRGV wildlife.

CHAPTER V

CONCLUSION

I was able to determine nesting success and nest-site selection of the Altamira Oriole and Northern Beardless-Tyrannulet in the Lower Rio Grande Valley, Texas. By studying more nests of these species than had been done in any previously published study, I was able to obtain samples that encompassed a wide range of habitat and population parameters.

Current populations of these two species appear stable, and, for the oriole, may be increasing since the low population numbers seen in the late 1980s and early 1990s. Although both species appear to require tall forests and woodlands, the tyrannulet is more of a habitat specialist, utilizing humid forests with abundant *Tillandsia* epiphytes. The preservation of both species will require the continued availability of large tracts of native Tamaulipan riparian brushland, like those in this study. Determining how to preserve these forests is beyond the scope of this paper, but continued reductions in the Rio Grande's water flow and the degradation of the forests in an historically water-dependent ecosystem point to some sort of water management as a potential solution.

The maintenance and enhancement of wetlands, particularly at El Morillo Banco and Santa Ana, is explicit in the Lower Rio Grande Valley and Santa Ana National Wildlife Refuges Interim Comprehensive Management Plan (U.S. Fish and Wildlife Service 1997), but El Morillo Banco's resaca was dry from 2001-2003. In addition, the flooding of Cattail Lakes at Santa Ana could be adjusted to allow flooding of nearby

forested areas rather than simply filling the lakes directly. Forests west and southwest of Cattail Lakes could potentially be improved if water could be input further "upstream" in the forest and allowed to eventually flow into the lakes, similar to the flooding pathway at Willow Lakes. But some flooding alternatives at Santa Ana are probably not feasible since much of the refuge is elevationally higher than the surrounding farmland, and overflow onto these lands would likely be an issue (J. Howland, U.S. Fish and Wildlife Service, personal communication).

Other detrimental human effects on LRGV wildlife, such as urbanization, further fragmentation, and increasing air and water pollution from both sides of the border deserve attention as urban centers grow with increased international trade. Recent disputes in U.S.-Mexico water allotments could be prolonged into the future, threatening the very idea of using water for recreational uses and habitat conservation.

Monitoring and research on these species should continue, and research in other parts of their ranges is needed to supplement these results and provide a more complete picture of their breeding ecology. Because life history studies have been biased toward temperate-zone species, some theories may not apply to tropical species (Martin 2004). We may begin to answer questions about phenomena such as delayed plumage maturation and breeding subadults in Altamira Orioles at the northern periphery of their range, in the LRGV, but surely much has yet to be learned about Altamira Orioles and the diverse Icteridae family throughout Central America and South America. Much avian conservation research has focused on Neotropical migrants (e.g., Hagan and Johnston 1992, Martin and Finch 1995), but year-round residents such as the Altamira

Oriole and Northern Beardless-Tyrannulet can likely be more rigorously studied than migratory landbirds that spend a significant portion of the year traveling.

In addition to investigating life history strategies and breeding biology of these birds, there is a great deal of research that can be done on responses to restoration, fragmentation, and source/sink population dynamics in the LRGV. The matrix of remnant brush tracts, recently replanted tracts, and parcels that have yet to be restored presents an excellent opportunity for future studies of this unique ecosystem.

LITERATURE CITED

American Ornithologists' Union. 1998. Check-list of North American birds. 7th Ed. American Ornithologists' Union, Washington, DC.

Anderson, A. H., and A. Anderson. 1948. Notes on two nests of the Beardless Flycatcher near Tucson, Arizona. Condor 50:163-164.

Baicich, P. J., and Harrison, C. J. O. 1997. A guide to the nests, eggs, and nestlings of North American birds. 2nd Ed. Academic Press, San Diego, CA.

Beck, M. J., and T. L. George. 2000. Song post foraging site characteristics of breeding Varied Thrushes in northwestern California. Condor 102:93-103.

Blair, W. F. 1950. The biotic provinces of Texas. Texas Journal of Science 2:93-117.

Braden, G. T. 1999. Does nest placement affect the fate or productivity of California Gnatcatcher nests? Auk 116:984-993.

Brandt, H. 1951. Arizona and its bird life. The Bird Research Foundation, Cleveland OH.

Brush, T. 1996. Current status of Altamira Orioles (*Icterus gularis*) in the Lower Rio Grande Valley, Texas. Report to the Lower Rio Grande Valley National Wildlife Refuge, Alamo, TX.

Brush, T. 1998a. A closer look: Altamira Oriole. Birding 30:46-53.

Brush, T. 1998b. Recent nesting and current status of Red-Billed Pigeon along the lower Rio Grande in southern Texas. Bulletin of the Texas Ornithological Society 31:22-26.

Brush, T. 1999. Current status of Northern Beardless-Tyrannulet and Tropical Parula in Bentsen-Rio Grande Valley State Park and Santa Ana National Wildlife Refuge, southern Texas. Bulletin of the Texas Ornithological Society 32:3-12.

Brush, T. 2000a. Audubon's Oriole, *Icterus graduacauda*. Texas Birds 2:4-9.

Brush, T. 2000b. Bronzed Cowbirds (*Molothrus aeneus*) still parasitize Hooded Orioles (*Icterus cucullatus*) in the Lower Rio Grande Valley of Texas. Bulletin of the Texas Ornithological Society 33:9-11.

Brush, T., and A. Cantu. 1998. Changes in the breeding bird community of subtropical evergreen forest in the Lower Rio Grande Valley of Texas, 1970s-1990s. Texas Journal of Science 50:123-132.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd Ed. Springer-Verlag, New York.

Campbell, L. 1995. Endangered and threatened animals of Texas: their life history and management. University of Texas Press, Austin, TX.

Cantu, A. 1996. Using the spot-mapping censusing technique to assess changes in breeding bird communities at Santa Ana National Wildlife Refuge, Alamo, Texas. M.Sc. thesis, University of Texas-Pan American, Edinburg, TX.

Carter, M. D. 1984. The social organization and parasitic behavior of the Bronzed Cowbird in south Texas. Ph.D. diss., University of Minnesota, Minneapolis, MN.

Carter, M. D. 1986. The parasitic behavior of the Bronzed Cowbird in south Texas. Condor 88:11-25.

Castillo, C. D. 1997. Effects of artificial flooding on the vegetation and avifauna of
riparian woodlands at Santa Ana National Wildlife Refuge, Hidalgo Co., Texas.
M.Sc. thesis, University of Texas-Pan American, Edinburg, TX.

Chase, M. K. 2002. Nest site selection and nest success in a Song Sparrow population:
the significance of spatial variation. Condor 104:103-166.

Clover, E. U. 1937. Vegetational survey of the Lower Rio Grande Valley, Texas.
Madroño 4:41-72,77-100.

Davis, L. I. 1940. Elm-ash association. Bird Lore 42:488-489.

Diamond, J. M. 1984. "Normal" extinctions of isolated populations, p. 191-246. *In* M.
H. Nitecki [ed.], Extinctions. The University of Chicago Press, Chicago, IL.

Dickey, D. R., and A. J. van Rossem. 1938. The birds of El Salvador. Field Museum of
Natural History Zoological Series 23.

Dijak, W. D., and F. R. Thompson. 2000. Landscape and edge effects on the
distribution of mammalian predators in Missouri. Journal of Wildlife
Management 64:209-216.

Eddy, M. R., and F. W. Judd. 2003. Phenology of *Acacia berlandieri*, *A. minuata*, *A.
rigidula*, *A. schaffneri*, and *Chloroleucon ebano* in the Lower Rio Grande Valley
of Texas during a drought. Southwestern Naturalist 48:321-322.

Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. The birder's handbook: a field guide
to the natural history of North American birds. Simon and Schuster, New York.

Enstrom, D. A. 1992. Breeding season communication hypotheses for delayed plumage maturation in passerines: tests in the Orchard Oriole, *Icterus spurius*. Animal Behaviour 43:463-472.

ESRI Inc. 2002. ArcMap 8.3, build 800. Environmental Systems Research Institute, Inc., Redlands, CA.

Fitzpatrick, J. W. 1983. *Tyrannus melancholicus*, p. 611-613. *In* D. H. Janzen [ed.], Costa Rican Natural History. The University of Chicago Press, Chicago, IL.

Fall, B. 1973. Noteworthy bird record from South Texas (Kenedy County). Southwestern Naturalist 18:244-247.

Flood, N. J. 1984. Adaptive significance of delayed plumage maturation in male Northern Orioles. Evolution 38:267-279.

Foster, M. S. 1987. Delayed maturation, neoteny, and social system differences in two manakins of the genus *Chiroxiphia*. Evolution 41:547-558.

Friedmann, H. 1925. Notes on the birds observed in the Lower Rio Grande Valley of Texas during May, 1924. Auk 42:537-554.

Friedmann, H. 1929. The cowbirds: a study in the biology of social parasitism. C. C. Thomas, Springfield, IL.

Friedmann, H. 1971. Further information on the host relations of the parasitic cowbirds. Auk 88:239-255.

Friedmann, H., L. F. Kiff, and S. I. Rothstein. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. Smithsonian Contributions to Zoology 235.

Gayou, D. C. 1995. Green Jay (*Cyanocorax yncas*). *In* A. Poole and F. Gill [eds.], The birds of North America, No. 187. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

Gehlbach, F. R. 1981. Mountain islands and desert seas: a natural history of U.S.-Mexico borderlands. Texas A&M University Press, College Station, Texas.

Gehlbach, F. R. 1987. Natural history sketches, densities, and biomass of breeding birds in evergreen forests of the Rio Grande, Texas, and the Rio Corona, Tamaulipas, Mexico. Texas Journal of Science 39:241-251.

Grimes, S. A. 1953. Black-throated Oriole (*Icterus gularis*) nesting in Texas. Auk 70:207.

Hagan, J. M. and D. W. Johnston [eds.]. 1992. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, DC.

Haskell, D. G. 1995. A reevaluation of the effects of forest fragmentation on rates of bird-nest predation. Conservation Biology 9:1316-1318.

Hathcock, C. R. 2000. Factors affecting the reproductive success in hosts of the Bronzed Cowbird (*Molothrus aeneus*) in the Lower Rio Grande Valley, Texas. M.Sc. thesis, University of Texas-Pan American, Edinburg, TX.

Hathcock, C. R., and T. Brush. 2004. Breeding decline and nest-site shift of the Altamira Oriole at Santa Ana National Wildlife Refuge, Texas. Southwestern Naturalist 49:33-38.

Hensler, G. L., and J. D. Nichols. 1981. The Mayfield method of estimating nesting success: a model, estimators, and simulation results. Wilson Bulletin 93:42-53.

Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54:427-432.

Hines, J. E., and J. R. Sauer. 1989. Program CONTRAST – A general program for the analysis of several survival or recovery rate estimates. U.S. Fish & Wildlife Service, Fish & Wildlife Technical Report 24.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. 2nd Ed. John Wiley & Sons, New York.

Howell, S. G., and S. Webb. 1995. A guide to the birds of Mexico and northern Central America. Oxford University Press, New York.

Jahrsdoerfer, S. E., and D. M. Leslie, Jr. 1988. Tamaulipan brushland of the Lower Rio Grande of South Texas: description, human impacts, and management options. U. S. Fish and Wildlife Service Biological Report 88(36).

James, F. C., and H. H. Shugart. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727-736.

Jaramillo, A., and P. Burke. 1999. New world blackbirds: the Icterids. Princeton University Press, Princeton, NJ.

Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651–661.

Johnson, K, and B. D. Peer. 2001. Great-tailed Grackle (*Quiscalus mexicanus*). *In* A. Poole and F. Gill [eds.], The birds of North America, No. 576. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

Jones, S. D., J. K. Wipff, and P. M. Montgomery. 1997. Vascular plants of Texas: a comprehensive checklist including synonymy, bibliography, and index. University of Texas Press, Austin, TX.

Joyce, F. J. 1993. Nesting success of Rufous-naped Wrens (*Campylorhynchus rufinucha*) is greater near wasp nests. Behavioral Ecology and Sociobiology 32:71-77.

Lack, D. 1954. The natural regulation of animal numbers. Oxford University Press, London.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

Lariviere, S. 1999. Reasons why predators cannot be inferred from nest remains. Condor 101:718-721.

Lonard, R. I., and F. W. Judd. 1991. Comparison of the effects of the severe freezes of 1983 and 1989 on native woody plants in the Lower Rio Grande Valley, Texas. Southwestern Naturalist 36:213-217.

Lonard, R. I., and F. W. Judd. 2002. Riparian vegetation of the lower Rio Grande. Southwestern Naturalist 47:420-432.

Lowther, P. E. 1995. Bronzed Cowbird (*Molothrus aeneus*). *In* A. Poole and F. Gill, [eds.], The birds of North America, No. 144. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

Marion, W. R. 1974. Status of the Plain Chachalaca in south Texas. Wilson Bulletin 86:200-205.

Martin, T. E. 1992. Breeding productivity considerations: What are the appropriate habitat features for management?, p. 455-473. *In* J. M. Hagan and D. W. Johnston [eds.], Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, DC.

Martin, T. E. 1993. Nest predation and nest sites: new perspectives on old patterns. Bioscience 43:523-532.

Martin, T. E. 2004. Avian life-history evolution has an eminent past: does it have a bright future? Auk 121:289-301.

Martin, T. E., and D. M. Finch [eds.]. 1995. Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues. Oxford University Press, New York.

Martin, T. E., and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64:507-519.

Martin, T. E., C. R. Paine, C. J. Conway, W. M. Hochachka, P. Allen, and W. Jenkins. 1997. BBIRD Field Protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT.

Mayfield, H. F. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255-261.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456-466.

Moldenhauer, R. R., and D. J. Regelski. 1996. Northern Parula (*Parula americana*). *In* A. Poole and F. Gill, [eds.], The birds of North America, No. 215. The

Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

National Climatic Data Center. [online]. 2003. McAllen Miller International Airport. <http://www.ncdc.noaa.gov/oa/climate/stationlocator.html> (2 December 2003).

Oberholser, C. H. 1974. The bird life of Texas. Volume 2. University of Texas Press, Austin, TX.

Pashley, D. N., C. J. Beardmore, J. A. Fitzgerald, R. P. Ford, W. C. Hunter, M. S. Morrison, K. V. Rosenberg. 2000. Partners in flight: conservation of the land birds of the United States. American Bird Conservancy, The Plains, VA.

Peer, B. D., and S. G. Sealy. 1999. Laying time of the Bronzed Cowbird. Wilson Bulletin 111:137-139.

Pettingill, O. S. 1942. The birds of a bull's horn acacia. Wilson Bulletin 54:89-96.

Phillips, A., J. Marshall, and G. Monson. 1964. The birds of Arizona. University of Arizona Press, Tucson, AZ.

Pleasants, B. Y. 1977. Ecological factors affecting the breeding dispersion patterns of some North American orioles (*Icterus*). Ph.D. diss., University of California, Los Angeles, CA.

Pleasants, B. Y. 1981. Aspects of the breeding biology of a subtropical oriole, *Icterus gularis*. Wilson Bulletin 93:531-537.

Pleasants, B. Y. 1993. Altamira Oriole (*Icterus gularis*). *In* A. Poole and F. Gill, [eds.], The birds of North America, No. 56. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

Proudfoot, G. A. 1996. Miniature video-board camera used to inspect natural and artificial nest cavities. Wildlife Society Bulletin 24:528-530.

Proudfoot, G. A. 2002. Two optic systems assist removal of nestlings from nest cavities. Wildlife Society Bulletin 30:956-959.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652-651.

Pyle, P. 1997. Identification guide to North American birds. Part I. Slate Creek Press. Bolinas, CA.

Renfrew, R. B., and C. A. Ribic. 2003. Grassland passerine nest predators near pasture edges identified on videotape. Auk 120:371-383.

Rich, T. D., C. J. Beardmore, H. Berlanga, P. J. Blancher, M. S. W. Bradstreet, G. S. Butcher, D. W. Demarest, E. H. Dunn, W. C. Hunter, E. E. Iñigo-Elias, J. A. Kennedy, A. M. Martell, A. O. Panjabi, D. N. Pashley, K. V. Rosenberg, C. M. Rustay, J. S. Wendt, T. C. Will. 2004. Partners in Flight North American Landbird Conservation Plan. Cornell Lab of Ornithology, Ithaca, NY.

Richardson, A. 1995. Plants of the Rio Grande delta. University of Texas Press, Austin, TX.

Robinson, S. K. 1985. Coloniality in the Yellow-rumped Cacique as a defense against nest predators. Auk 102:506-519.

Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987-1990.

Rohwer, S., S. D. Fretwell, and D. M. Niles. 1980. Delayed maturation in passerine plumages and the deceptive acquisition of resources. American Naturalist 115:400-437.

Rothstein, S. I. 1977. Cowbird parasitism and egg recognition of the Northern Oriole. Wilson Bulletin 1989:21-32.

Rothstein, S. I., J. Verner, and E. Stevens. 1984. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic Brown-headed Cowbird. Ecology 65:77-88.

Rupert, C. E. 1997. Breeding densities and habitat of riparian birds along the Lower Rio Grande, Texas. M.Sc. thesis, University of Texas-Pan American, Edinburg, TX.

Scott, D. M. 1991. The time of day of egg laying by the Brown-headed Cowbird and other icterines. Canadian Journal of Zoology 69:2093-2099.

Sealy, S. G. 1980. Breeding biology of Orchard Orioles in a new population in Manitoba. Canadian Field Naturalist. 94:154-158.

Sealy, S. G., and D. L. Neudorf. 1995. Male Northern Orioles eject cowbird eggs: implications for the evolution of rejection behavior. Condor 97:369-375.

Selander, R. K. 1965. On mating systems and sexual selection. American Naturalist 99:129-141.

Sennett, G. B. 1878. Notes on the ornithology of the Lower Rio Grande of Texas from observations made during the season of 1877. Bulletin of the U.S. Geological Geographic Survey 4:1-66.

Shackleford, C. E., E. R. Rozenburg, W. C. Hunter, and M. W. Lockwood. 2000. Migration and the migratory birds of Texas: who they are and where they are going. 2nd Ed. Texas Parks and Wildlife PWD BK W7000-511 (2/00).

Skutch, A. F. 1954. Life histories of Central American birds. Pacific Coast Avifauna No. 31. Cooper Ornithological Society, Berkeley, CA.

Skutch, A. F. 1997. Life of the flycatcher. University of Oklahoma Press, Norman, OK.

Smith, A. P. 1910. Miscellaneous bird notes from the Lower Rio Grande. Condor 12:93-103.

Smith, N. G. 1983. *Zarhynchus wagleri*, p. 614-616. *In* D. H. Janzen [ed.], Costa Rican Natural History. The University of Chicago Press, Chicago, IL.

SPSS Inc. 2001. SPSS for Windows: release 11.0.1. SPSS Inc., Chicago, IL.

SPSS Inc. 2003. SPSS for Windows: release 12.0.0. SPSS Inc., Chicago, IL.

Sternberg, M. A. 2001. Comparison of rodent communities of native brushland, replanted, and secondary succession sites in the Lower Rio Grande Valley of Texas. M.Sc. thesis, University of Texas-Pan American, Edinburg, TX.

Stiles, F. G., and A. F. Skutch. 1989. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, NY.

Sutton, G. M. and T. D. Burleigh. 1940. Birds of Tamazunchale, San Luis Potosi. Wilson Bulletin 52:221-233.

Sutton, G. M., and O. S. Pettingill. 1943. The Alta Mira Oriole and its nest. Condor 45:124-132.

Tenney, C. R. 2000. Northern Beardless-Tyrannulet (*Camptostoma imberbe*). *In* A. Poole and F. Gill, [eds.], The birds of North America, No. 519. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

Terborgh, J. 1992. Perspectives on the conservation of Neotropical landbirds, p. 7-12. *In* J. M. Hagan and D. W. Johnston [eds.], Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, DC.

Texas Natural Resource Conservation Commission [online]. 2002. State of the Rio Grande and the environment of the border region. TNRCC Strategic Plan, Fiscal Years 2003-2007, Volume 3, SFR-035C/02. <http://www.tnrcc.state.tx.us/ admin/topdoc/sfr/035_02/035_02_vol3.html> (16 June 2004).

Texas Organization For Endangered Species. 1995. Endangered, threatened, and watch list of vertebrates of Texas, fourth revision. Publication 10. Texas Organization for Endangered Species, Austin, TX.

Thompson, F. R., III, and D. E. Burhans. 2003. Predation of songbird nests differs by predator and between field and forest habitats. Journal of Wildlife Management 67:408-416.

Thompson, F. R., III, W. Dijak, and D. E. Burhans. 1999. Video identification of predators at songbird nests in old fields. Auk 116:259-264.

U.S. Fish and Wildlife Service [online]. 1997. Lower Rio Grande Valley and Santa Ana National Wildlife Refuges Interim Comprehensive Management Plan. U.S. Fish

and Wildlife Service, Alamo, TX. <http://library.fws.gov/CMP/ index_cmps.htm> (1 June 2004).

U.S. Geological Survey. 2000. Species at risk: Pre-proposal package, fiscal year 2000. U.S. Geological Survey, Reston, VA.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

van Rossem, A. J. 1936. Notes on birds in relation to the faunal areas of south-central Arizona. Transactions of the San Diego Society of Natural History 8:121-148.

Vickery, P. D., P. L. Tubaro, J. M. Cardoso da Silva, B. G. Peterjohn, J. R. Herkert, and R. B. Cavalcanti. 1999. Conservation of grassland birds in the western hemisphere. Studies in Avian Biology 19:2-26.

Vora, R. S. 1990. Plant communities of the Santa Ana National Wildlife Refuge, Texas. Texas Journal of Science 42:115–128.

Vorhies, C. T., R. Jenks, A. R. Phillips. 1935. Bird records from the Tucson region, Arizona. Condor 37:243-247.

Webster, F. S. 1962. South Texas region. American Birds 16:489-493.

Webster, F. S. 1972. South Texas region. American Birds 26:875-878.

Webster, F. S. 1974. South Texas region. American Birds 28:922-925.

Webster, M. S. 1994. The spatial and temporal distribution of breeding female Montezuma Oropendolas: effects on male mating strategies. Condor 96:722-733.

Wiens, J. A., and J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecological Monographs 51:21-41.

Zar, J. H. 1996. Biostatistical analysis. 3rd Ed. Prentice-Hall, Upper Saddle River, NJ.

VITA

SCOTT MICHAEL WERNER
16010 Rose Ave
Monte Sereno, CA 95030

EDUCATION

Master of Science, Wildlife and Fisheries Sciences, Texas A&M University, 2004.

Bachelor of Science, Ecology and Evolution, University of California, Santa Barbara,
1996.

EXPERIENCE

2001 – 2004. Graduate Assistant, Non-teaching/Teaching. Department of Wildlife and
Fisheries Sciences, Texas A&M University.

2000-2001. Biologist (Wildlife). Santa Clara Valley Water District, San Jose, CA.

2000. Field Assistant. Integrated Hardwood Range Management Program, University
of California Cooperative Extension, San Luis Obispo, CA.

1999. Primary Bander. Redwood Sciences Laboratory, U. S. Forest Service, Arcata,
CA.

1998-1999. Biologist. San Bernardino County Museum, Redlands, CA.

1997. Field Assistant. School of Forestry, Northern Arizona University, Flagstaff, AZ.

1997. Field Assistant. Integrated Hardwood Range Management Program, University
of California Cooperative Extension, San Luis Obispo, CA.

1996. Research Assistant. Department of Ecology, Evolution, and Marine Biology,
University of California, Santa Barbara.