NEST SITE SELECTION AND PARTITIONING AMONG SYMPATRIC WHITE-WINGED, MOURNING, AND INCA DOVES IN MASON, TEXAS

A Thesis

by

HEATHER ALEXIS MATHEWSON

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 2002

Major Subject: Wildlife and Fisheries Sciences

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ABSTRACT

Nest Site Selection and Partitioning Among Sympatric White-winged, Mourning,
and Inca Doves in Mason, Texas. (August 2002)
Heather Alexis Mathewson, B. S., Texas A&M University
Chair of Advisory Committee: Dr. Nova J. Silvy

Local natural communities can be negatively impacted by native species' range expansion into previously uninhabited areas. Recently, white-winged doves (*Zenaida asiatica*) have expanded their geographical range into areas where mourning (*Z. macroura*) and Inca (*Columbina inca*) doves have traditionally nested. The first record of breeding white-winged doves in Mason, Texas was in 1992. Mourning doves once nested throughout Mason but local residents have observed a sharp decline over the last decade. Several studies have focused on descriptions of individual species' nesting habits yet few studies exist that compare sympatric populations of these dove species. With the invasion of white-winged doves into new geographic locations, the potential for competition exists between them and smaller Columbids. The objectives of my study were to: (1) determine spatial distribution of the 3 dove species in Mason, Texas; (2) examine the effect of nesting aggregations of white-winged doves on the other 2 species; and, (3) compare nest-site characteristics, nest-site partitioning, and assess the role of interspecific competition on nest-site selection. Nest searching, monitoring, nest-site characterizations, and vegetation measurements were conducted during June–August 2001.

White-winged doves ($n = 89$) appeared to select residential and urban centers over the rural periphery of the town (97%), while 81% of the mourning dove nests ($n = 27$) were located on the outskirts of town. Inca doves ($n = 20$) appeared to nest equally in both locations. Of the 3 dove species, mourning dove nest success (37%, $n = 27$) was low, white-winged dove nest success was 50% ($n = 78$) and Inca dove nest success (62%, $n = 21$) was high. White-winged doves often nested near another white-winged dove nest, yet nest success increased with distance from another active nest. Nest-site characteristics indicated differential resource use, therefore, it is suggested the 3 dove species were partitioning nest sites. While it appears white-winged doves may be excluding mourning doves from residential and urban areas, future research is needed to determine whether this is detrimental to the mourning dove population.

I can not possibly thank my parents, Dr. Christopher C. and Mrs. Janet M. Mathewson, enough for their love and belief in me. I am following in my father's footsteps and my mother will always be my best friend. Many, many thanks to Glenn and Jennifer Mathewson, and to our new family member, Kaia. And, of course, to Kacei and Stephanie.

ACKNOWLEDGEMENTS

There are many people I would like to thank, for without them these last two years would not have been as successful. I have been honored to work with Dr. Nova J. Silvy. I am especially grateful for his guidance, patience, continuous support, and friendship. Many thanks to his beautiful family, Val and Beth. Thank you to my committee, Dr. Markus J. Peterson and Dr. Don Davis, for their time and support. Without T. Wayne Schwertner, I would have never stumbled upon this project. Texas Parks & Wildlife at Mason Mountain Wildlife Management Area helped support me by giving me a place to live and offering equipment. Thank you to the biologists at Mason Mountain. Thank you to Todd Pilcik who was a key player in initiating white-winged dove research in Mason, Texas. Stephen Webb conducted the research on white-winged doves in Mason during the summer of 2000.

Thank you to the community of Mason, who graciously allowed me to trample across their yards and schools. I could not have picked a better town with better people to spend the summer with. Thank you for the lunches, the visits, the encouragement, and the cokes.

Thanks to the faculty and staff of the Wildlife & Fisheries Department for their encouragement, support and for everything they taught me: Dr. R. Douglas Slack, Dr. Jane Packard, Dr. Roel Lopez, , Dr. Keith Arnold, Dr. Robert D. Brown and Dr. Bill Neill. Many thanks to Ann Williams, Janice Crenshaw, Carol Gaas, and Shirley

Konecny for always being there to rescue me. Thanks to Dr. Clifton Griffin and Dr. Rick Giardino in the Office of Graduate Studies.

Thank you to Jennifer Cearley for assistance in field work and data entry. Shane Horrocks, Shawn Gray, Carrie Proctor, Michael Chambless, Molly Melton, Dale Kubenka, Robert Powell, Stacey Allison, Dawn Sherry and Chris Niebuhr provided additional assistance with field work, data entry, and presentation preparations. Thank you to Debbie Scott, Chris Antenen, Alec MacDonald and Lacey Tlustos who assisted with early field work before the focus of my thesis changed. Thanks to Cristina Martinez, a fellow white-winged dove researcher.

I owe the following individuals many, many thanks for each part they have played in my life: Autumn Lind, Andrea Gilkinson, Holly Stephens, Robert Andrew Powell, Stacey Allison, Richard Heilbrun, Dawn Sherry, Karl Kosciuch, Ryan Jones, Dustin Jones, Dale Kubenka, Jason Sebesta, Chris Niebuhr, Molly Melton, Thomas Dixon, Nikki Pederson, Amy O'Rourke, Elissa Eppes, Stephanie Wilson, Dianna Collier, Lysa Maki, Emily Williams, TJ Williams, Britt Heidinger, TJ Fontaine, Paul Martin, and Dr. Tom E. Martin. Thank you to all the undergraduate students I was lucky to teach or to work with and to the Texas A&M Student Chapter of The Wildlife Society.

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INTRODUCTION

Local natural communities can be negatively impacted by the invasion or introduction of nonnative species (Case and Bolger 1991, Lodge 1993, Voeten and Prins 1999, Rissler et al. 2000, Mooney and Cleland 2001). Equally detrimental may be native species expanding their range into previously uninhabited areas as a result of altered agricultural practices, landscape fragmentation, urbanization, and other reasons (Bock and Lepthien 1976, Minot and Perrins 1986, Hahn and Hatfield 1995, Kennedy and White 1996, Dark et al. 1998, Husak and Maxwell 2000, Ford et al. 2001). For example, spotted owl (*Strix occidentalis*) populations in California may be negatively impacted by the rapid range expansion of the congeneric barred owl (*Strix varia*), a dominant competitor with the ability to adapt to disturbed habitats (Dark et al. 1998). Expanding populations of house wrens (*Troglodytes aedon*) may be contributing to declining Bewick's wren (*Thryomanes bewickii*) abundances by interference competition for nest sites (Kennedy and White 1996). One of the primary factors associated with range expansion is urbanization (Bock et al. 1976, Kennedy and White 1996). Factors associated with human settlements create an ecosystem supportive of species that benefit from human resources while selecting against many native species (Engels and Sexton 1994, Friesen et al. 1995, Marzluff et al. 1998). Exotic avian species such as European starling (*Sturnus vulgaris*) and house sparrow (*Passer domesticus*) account for much of the biomass of urban bird communities (Beissinger and Osborne 1982, Marzluff et al. 1998). Additionally, many columbid species show preference

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This thesis follows the style of the Journal of Wildlife Management.

towards human settlements (Johnston 1960, Mueller 1992, Small and Waggerman 1999).

In the Columbiform complex, mourning doves (*Zenaida macroura*) are widely distributed throughout North America, including all of Texas (Sayre and Silvy 1993), and Inca doves (*Columbina inca*) inhabit the majority of Texas year-round (Mueller 1992). Other dove species traditionally inhabit south Texas, however, recently there has been an expansion in range of white-winged doves (*Z. asiatica*). Prior to 1965, 95% of the breeding population of white-winged doves in Texas nested in the Lower Rio Grande Valley (LRGV; Cottam and Trefethen 1968). During the last 50 years, white-winged doves began expanding their range northward into the central Trans-Pecos region of Texas (Small et al. 1989), Kleberg County, Texas (Hayslette and Hayslette 1999), San Antonio, Texas (West 1993), Utah (Behle 1976), and Colorado (Braun et al. 1979). Nesting habitats of dove species have been described for individual species (Johnston 1960, Cottam and Trefethen 1968, Jenks 1983, Mueller 1992, Sayre and Silvy 1993, West 1993), yet few studies examine coexistence of columbids (Passmore 1981, Cunningham et al. 1997). In parts of Texas, white-winged dove ranges now overlap with mourning and Inca dove populations. The impact expanding white-winged doves range might have on local avian guilds has not been examined.

Mason, Texas, located in Mason County, in the central Hill Country, is a town of approximately 2,000 residents (Fig. 1). Mason County is within the historical nesting range of both mourning (Sayre and Silvy 1993) and Inca doves (Mueller 1992). White-winged doves were first documented breeding in this county in 1992 (T. Pilcik, Texas Parks and Wildlife, personal communication). Local residents reported a dramatic and

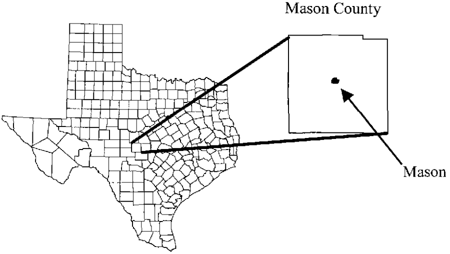

Fig. 1. Location of Mason and Mason County in Texas (map courtesy of T. Pilcik and T. W. Schwertner, Texas Parks and Wildlife).

sudden increase in white-winged dove numbers over the last decade. Call count and nesting data from June 2000, conducted by Texas Parks & Wildlife (TPW), indicate a distinct segregation of nesting white-winged and mourning doves; white-winged doves appeared to nest exclusively in urban centers while mourning doves nested primarily at the town's peripheries (T. W. Schwertner, TPW, personal communication). The partitioning of nest sites in the town of Mason presents an opportunity to examine the ecological impact of white-winged dove populations on the availability of nesting habitat for other columbids.

Interspecific Competition

Ecological guilds comprise local species that temporally and spatially exploit common resources (Wiens 1989*a*, Begon et al. 1996). A fundamental question of community ecology focuses on how coexisting guild members interact and partition resources (Wiens 1989*a*). Niche overlap theory states that when resources are limited, and guild members share a broad range of resources, then species should become more specialized in order to decrease competition with the other members of the guild (Wiens 1989*a*, Begon et al. 1996). The primary resources, or niche dimensions, are time, diet, and habitat. Schoener (1974) suggested that habitat typically is more important than diet, which in turn is more often important than temporal differences. Most species exhibit niche differentiation in more than one dimension (Schoener 1974), whereas segregation along only 1 dimension implies considerable overlap along another dimension; thus failing to reduce competition (Pianka 1974, May 1975). The majority of niche overlap studies in avian species focused on resource partitioning of food types

(Schoener 1965, Holmes and Pitelka 1968, Arlettaz et al. 1997, Wathne et al. 2000) and partitioning of habitat in relation to foraging (MacArthur and Pianka 1966, Edington and Edington 1972, Snow and Snow 1972, Cody 1974, Bosakowski et al. 1992, Craig and Beal 2001). Few studies have addressed partitioning of space in relation to habitat use or nest sites (Pulliam and Mills 1977, Guthrey et al. 2002).

There generally are 2 types of interspecific competition, interference and exploitative. Interference competition requires a direct physical interaction, whereas exploitation is an indirect effect by exploiting resources, which limits their use by other species (Wiens 1989*b*). Exploitative competition further can be classified as preemptive competition with regards to space as a resource that can not be occupied until the current owner has vacated the space (Schoener 1983). Regardless of the type of competition, the outcome is that subdominant species are negatively impacted through decreased reproduction or survival (Wiens 1989*b*).

Interspecific competition, either interference or exploitative, is difficult to test experimentally (Schoener 1974). Interference competition for space has been directly tested by removal experiments (Connell 1961, Hairston 1986, Martin and Martin 2001*a*), or by exploiting the aggressive responses of territoriality through intentional provocation by auditory or visual stimulus (Orians and Willson 1964, Sherry and Holmes 1988, Martin et al. 1996). Oftentimes, however these experiments are not possible and conclusions are inferred or deduced based on observed results of resource measurements (Arlettaz et al. 1997, Voeten and Prins 1999, Rissler et al. 2000).

A fundamental question regarding interspecific competition for nesting sites is whether nest sites are limiting. Cavity nest sites may be limiting (Collias and Collias 1984, Li and Martin 1991) but, traditionally, open-cup nest sites were considered readily available (Wiens 1989*b*). However, results of experimental studies have suggested that open-cup nesting sites might actually be limiting (Martin and Martin 2001*b*). Habitat fragmentation, predators, or competitive species may be factors contributing to limited nest site availability (Cody 1985). In response, species may be forced into sub-optimal habitat (Brown 1969, Fretwell 1972).

It is assumed that given complete availability of habitat choices, an individual would select the habitat that provides the greatest probability for increased fitness (Brown 1969). This optimal habitat is often determined when the frequency or proportion of a chosen habitat characteristic is greater than the frequency or proportion of a habitat characteristic selected at chance in available habitat (West et al. 1993, Martin 1998, Hooge et al. 1999). High reproductive success in these preferred habitats would support the assumption that individuals choose optimal habitat. However, reproductive success is not always highest in the preferred habitat signifying a constraint on nest-site selection (West et al. 1993). Three possible constraints could be (1) interspecific competition, (2) high densities of predators in optimal habitats, and/or (3) high nest densities of ecologically similar species.

History of White-winged Doves in Texas

The white-winged dove ranges from Central America to its historic northern extension in southern Texas, New Mexico, and Arizona. Approximately 12 subspecies have been described, the western subspecies (*Z. a. mearnsi*), located in Arizona, New Mexico and possibly some of western Texas, and the eastern subspecies (*Z. a. asiatica*) inhabiting much of south Texas and northeast Mexico, are the most numerous and widely-distributed (Saunders 1968). Once abundant in the LRGV, the white-winged dove experienced great population fluctuations during the 1900s (Cottam and Trefethen 1968). Historically, the breeding habitat of the eastern subspecies of the white-winged dove was limited in Texas to the LRGV, including Cameron County, and parts of Willacy, Hidalgo, and Starr counties (Cottam and Trefethen 1968). However, over the last several decades their range has increased dramatically.

Agricultural practices in the LRGV in the early 1900s initially augmented the doves' food and water supply. In 1923, there was an estimated peak of 4–12 million birds (George et al. 2000). Approximately 80% of the breeding population of the eastern subspecies relied on Taumalipas thorn scrub community, described as dense brush with small (3–10 m height) trees, in the LRGV (Cottam and Trefethen 1968, George et al. 2000). The climate is humid, warm, and mild, with minimum temperatures rarely below freezing and maximum temperatures in June through August, the breeding season for white-winged dove (George et al. 2000).

Increased agricultural development for production of corn, cotton, and sorghum, eventually decimated the native thorn scrub habitat. By 1942, over 200,000 ha of native vegetation had been cleared for development (Marsh and Saunders 1942). Concerned over the decline of white-winged dove populations, biologists began stringent monitoring of hunting and habitat restoration and populations increased in part due to citrus production (Cottam and Trefethen 1968). Citrus production in the LRGV increased after 1920, and white-winged dove readily adapted to nesting in citrus groves (Brown et al. 1977). Use of citrus groves increased in the 1940s, and by 1950 an estimated 90% of white-winged doves in the LRGV were using citrus for nesting (Cottam and Trefethen 1968; Fig. 2*a*). However, citrus trees are highly susceptible to destruction from freezes, and severe winters in 1951, 1962, 1983, and 1989 brought about a population decline of approximately 40-90% (Cottam and Trefethen 1968). By 1970, only 60% were using citrus for nesting and by the 1980s, less than 1% of the native nesting habitat existed in the LRGV, most owned by state or federal government (George et al. 2000).

Population levels in the LRGV continued to decline while numbers increased farther north in Texas (Cottam and Trefethen 1968, Purdy 1983, George 1991). Based on call-count data, from 1976–1997, white-winged dove use of urban areas significantly increased as use of citrus groves declined (Small and Waggerman 1999). The highest abundances now occur in association with human settlements (Brown et al. 1977). By the 1990s, approximately 50% of the white-winged dove population north of the LRGV was nesting in San Antonio (Fig. 2*b*; West et al. 1993). Additionally, there have been reports of nesting white-winged doves as far north as Fort Worth and Lubbock and towards the southeastern portions of Texas (T. Pilcik, TPW, personal communication). White-winged dove range expansion continues within towns and intermediate urban settings across Texas, Oklahoma, Colorado, Arizona and into other states.

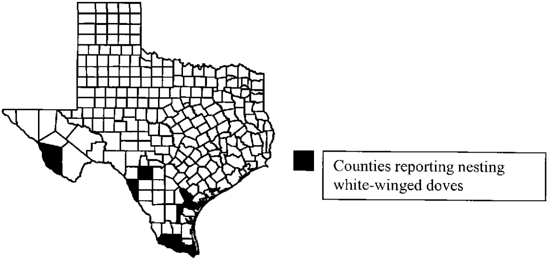

Fig. 2*a*. Counties reporting white-winged dove nesting activity in 1950s. Map courtesy of T. Pilcik, Texas Parks and Wildlife.

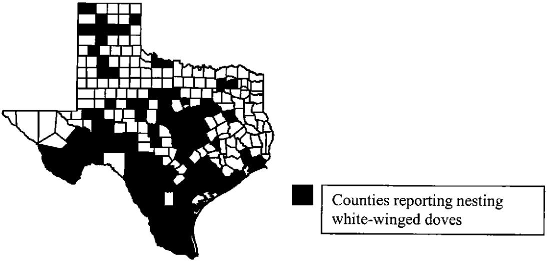

Fig. 2*b*. Counties reporting white-winged dove nesting activity in 1990s. Map courtesy of T. Pilcik and T. W. Scwertner, Texas Parks and Wildlife.

Nesting Ecology

Amongst the columbids in Texas, white-winged doves are larger (29 cm in length, 170 g.; Oberholser 1974), mourning doves are described as medium sized (22.5–34 cm in length; Mirarchi and Baskett 1994), and Inca doves are smallest (18–23 cm in length, 30–58 g; Mueller 1992). White-winged and Inca doves have similar distributions, however, white-wings extend farther into Central and South America. Both these species have expanded their geographic ranges over the last few decades (Mueller 1992, West et al. 1993). Mourning doves are distributed nation wide (Mirarchi and Baskett 1994).

Feeding and Foraging.—Columbids are granivorous and primarily forage on the ground. All 3 species rely heavily on agricultural grains, and bird feeders (Mueller 1992). Fruit may comprise an important part of doves' diet, especially white-winged doves in desert habitats where water may be scarce (MacMillian and Trost 1966). White-winged doves regularly perch on feeders above ground or on cacti in their western distribution (Wolf et al. 2002). Mourning and Inca doves feed mainly on the ground avoiding heavy vegetation that may interfere with their ability to detect predators. Additionally, they avoid heavy ground litter due to their foraging strategy of visually searching for seeds. Other ground feeders may probe or scratch the ground to locate food (Davison and Sullivan 1963, Lewis 1993). All 3 dove species join intra- and interspecific feeding flocks. White-winged doves form large gregarious foraging flocks (Cunningham 1986). Oftentimes, mourning and Inca doves can be seen foraging together, especially in backyards with bird feeders (personal observation). Doves require large quantities of water and are the only bird family with suction ability, whereas other birds must continuously lift their bills in order to swallow water (MacMillan and Trost 1966). The amount of water necessary to sustain doves is inversely related to body size, with white-winged doves requiring less and Inca doves requiring more, thus making them dependent on readily available water sources (MacMillan and Trost 1966).

Territoriality and Spacing.—White-winged and mourning doves only exhibit aggressive displays during nest building, egg laying, and early incubation. Sayre and Silvy (1993) found that mourning doves nesting in close proximity rarely have similar initiation dates. Male mourning doves are known to chase conspecifics out of their territory (Jackson and Baskett 1964, Sayre et al. 1993). Inca doves defend territories against conspecifics infrequently and only when provoked. Territoriality might increase as the nesting stage progresses. At communal feeding grounds, Inca doves reportedly retreat from mourning doves (Johnston 1960).

Territory size may be density-dependent (Swanson 1989). Historically, white-winged doves nested in colonies, although little is known about the exclusivity of this pattern. The eastern subspecies nested in colonies in the LRGV, but the western subspecies nested singly in the desert habitat where nesting substrates are widely spaced (Cottam and Trefethen 1968). Evidence suggests that white-winged doves nesting in San Antonio were distributed in colonies (West et al. 1993). Mourning doves nest solitarily but in high population densities, and nests may be as close as neighboring trees (personal observation). Inca doves maintain more of a distance during nesting, as much as 27–63 m (Mueller1992).

Breeding and Nesting.—Doves may be monogamous throughout a breeding season and the pair bond may remain intact over consecutive years (Goodwin 1983, Sayre et al. 1993). White-winged doves have a narrow time frame for nesting, usually April–August (Passmore 1981). Mourning dove nesting varies geographically from March–October (Sayre and Silvy 1993), and Inca doves nest year round (Oberholser 1974). Reproductive success depends on the ability of a pair to produce multiple broods over a breeding season (Westmoreland et al. 1986).

Courtship consists of species-specific coos and displays. Males usually select the nest site and collect material while the females construct the nest. The length of time required to build a nest is variable. Characteristic of most columbids, doves build twiggy platform nests, usually in trees or shrubs (Goodwin 1983). Reuse of old nests, or use of other species' nests, is prevalent in mourning doves (McClure 1943, Swank 1952) and white-winged doves (Saunders 1940, Cottam and Trefethen 1968). Investing little time or effort in constructing a nest or reusing an old nest may be a strategy for reducing the length of the nesting cycle, which is important for multiple brooding species (Westmoreland et al. 1986).

All columbids are determinate layers, with a clutch size of 2 eggs (Goodwin 1983, Westmoreland et al. 1986). Incubation begins immediately after the first egg is layed. Both sexes incubate eggs for approximately 14 days, and usually remain on the nest constantly. The male relieves the female in the late morning, remaining on the nest through the day, is then relieved by the female in the evening. Brooding of nestlings also is performed on the same schedule, with the adults returning to feed young (Johnston 1960, Cottam and Trefethen 1968, Mueller 1992, Mirarchi and Baskett 1994). Continuous nest attentiveness may increase embryo and nestling growth rate, thus shortening the time for brood rearing (Westmoreland et al. 1986). Additionally, shortened nesting cycles and continuous nest attentiveness may decrease predation (Westmoreland et al. 1986).

Nestlings are fed crop milk, which is a substance created in the crop of the adult by the sloughing of desquamated cells (Beams and Meyer 1931). It has been suggested that cropmilk production contributes to the success of doves, in that they do not have to rely on insect availability (Goodwin 1983). Nestling growth rate is fast and varies in length for all species according to environment, disturbances, or individuals.

Nest Site Selection.—All 3 species show a preference for urban parks, and residential areas (Johnston 1960, Cottam and Trefethen 1968, Quay 1982, Mueller 1992, West 1993, Mirarchi and Baskett 1994). Within urban communities, white-winged doves may select for residential areas <50 years rather than commercial or industrial zones (West et al. 1993). In human settlements, white-winged doves nest in large, sturdy trees with dense foliage that provide ample cover and shade. Most often these trees include pecan (*Carya illinoensis*), live oak (*Quercus virginiana*), and ash (*Fraxinus* spp.), as well as ornamentals (Nilsson 1943, Cottam and Trefethen 1968, West et al. 1993). Live oak and Arizona ash (*Fraxinus velutina*) were preferred in San Antonio (West 1993).

Mourning doves are generalists when it comes to selecting nest sites and often make use of man-made structures for nesting (Sayre and Silvy 1993). They select various deciduous trees, evergreens, shrubs, and vines in shelterbelts, citrus groves, and pecan orchards (Griffin 1994), and in grassland prairies they nest on the ground (McClure 1943, Sayre and Silvy 1993). Mourning doves appear to prefer suburban areas such as residential, golf courses, and parks (Blair 1996). Of great importance to nesting success may be structural stability (Coon et at. 1981), which can be located in a variety of substrates. Live oaks may be a species favored by mourning doves because they provide horizontal structure and they retain leaves year-round (Swank 1955, Grue 1977).

In 1889, the first Inca dove was recorded in Austin, Texas, and shortly thereafter, their prevalence in south Texas urban areas increased (Bent 1932). Prior to urbanization, little is known of their native habitat (MacMillian and Trost 1966). Johnston (1960) reports that for Inca doves, the exact nest site may not be as important as the general requirements of open areas and tall vegetation for cover, which are typical descriptions of urban parklands and residential areas. Inca doves also are known to make use of human structures for nest sites and their selection of trees is variable (Mueller 1992). They are sensitive to cold weather and therefore select microhabitats in direct sunlight. There is some indication of a preference for live oaks with little understory (Johnston 1960). Inca doves will breed year-round and live oaks probably provide them necessary cover since they maintain their leaves year-round.

Objectives

The purpose of this study was to investigate how a newly established population of white-winged doves influences ecologically similar native species, mourning and Inca doves, during their breeding season in Mason, Texas during June–August 2001. I examined the effect of interspecific competition on nest-site selection by measuring resource partitioning in nest-site characteristics. If differences in structure or vegetation characteristics exist between nest sites for individual species, then I assumed that differences minimized competition for nest sites. Specifically, I will (1) discuss spatial distribution of the dove species in Mason, Texas and delineate macrohabitat use for each, (2) examine the effect of spatial distribution and aggregations of nests on nesting success, (3) describe characteristics of nesting trees selected by individual dove species, (4) examine partitioning of nest site selection among the 3 dove species, (5) assess the role of interspecific competition on differential resource use (i.e. nest sites) of species under sympatric and allopatric conditions, and (6) discuss the theoretical application of niche overlap to a community of sympatrically nesting columbids.

STUDY SITE

This study was conducted in Mason, Texas, located in central Mason County (30.75° N, 99.23° W). This area is on the Edwards Plateau at an elevation of 435 m. From June-August, the average maximum temperature is 34.8°C and average minimum is 18.8°C. The climate is temperate with average monthly rainfall during these months ranging from 40.3–82.8 mm. Mason is approximately 775 ha and the human population exceeds 2,000 yet remains relatively stable.

Study sites were selected based on accessibility to property. City property, including the schools, golf course, city park, cemetery, and historical buildings were selected. Additionally, privately owned establishments, such as residential properties and churchyards, often with limited accessibility, were included with owner consent.

Marzluff et al. (2001) defines standard terminology for urban ecological studies and according to which, Mason is considered suburban and grades into rural or exurban areas. A 4-lane highway intersected Mason to the north and passes by the center courtyard. The courtyard is approximately 2.2 ha and dominated by mature pecans. Light commercial and basic service buildings surround the courtyard and are dominated by ornamental trees, pecans, small live oaks, and manicured shrubs. Land-cover is manicured lawns, roads, and concrete parking lots and side walks. Human disturbance is high and a sprinkler system and a water faucet available for public use in the courtyard continuously provided water. Within 1 or 2 blocks the landscape grades into church lots, small city parks, school property and residential areas also with high human disturbance. The schools and parks are characterized by dominant tree species of pecan, American elm (*Ulmus americana*), silver maple (*Acer saccharinum*), and live oak. The 16.5 ha schoolyard has some wooded, brushy creek areas, adjacent to expansive and maintained grassy areas used for recreational purposes. Church lots and the smaller city park are comprised of interspersed trees, predominately pecan and live oak, amongst mixed manicured lawns, parking lots, and taller grassy areas. Residential areas consist of mature pecan, silver maple, and ornamental shade tress interspersed with live, water (*Quercus nigra*), post (*Q. stellata*), and Spanish oak (*Q. falcata*) and manicured shrubs. Land-cover was predominately lawns maintained by sprinklers, sidewalks, and roads. Many residencies had bird feeders readily available.

Rural and exurban sites are primarily located on the periphery of town, some are proximal to homesteads, but, as opposed to the residential sites, considerable expanses of grazed or unmanaged land are interspersed amongst houses. Two sites were located on private ranches. Cacti (Cactaceae), honey mesquite (*Prosopis glandulosa*), and live oak dominated rural sites. The terrain was rocky with thick brush, few manicured yards, and mostly grazed fields. The large city park and golf course is on the edge of town and surrounded by agricultural, rangeland, or rural homesteads. Mature pecans interspersed with live oaks and American elms dominate the city park and land-cover is maintained lawns and taller, natural grassland areas. An impenetrable wooded, brushy creek area with foot trails borders the park. The golf course is sparsely vegetated with small, immature trees and a few large live oaks.

MATERIALS AND METHODS

In 2000, 44 points were established throughout Mason, Texas, including light commercial, residential, recreational, and rural/exurban zones. Call counts conducted at these points were used to determine the distribution of doves within Mason. Call counts were conducted on 12–14 June 2001, during the supposed peak of breeding for all 3 dove species.

For determination of landscape distribution of nest sites, I divided the study sites into peripheral and central, based upon their proximity to the center of Mason, Texas. A site was classified as peripheral if ≤ 2 cardinal directions were adjacent to any residential or commercial areas. These sites were adjacent to or included agricultural or rangelands. The central locations were classified as suburban (Marzluff et al. 2001) and included the center square and light commercial area, church lots, schoolyard, and residential lots.

Nest Searching and Monitoring

White-winged, mourning, and Inca dove nests were located primarily by strategically searching potential nesting sites (e.g. all trees and shrubs) within the study sites. Applicable techniques using behavioral cues and precautions for minimizing researcher-induced disturbances were followed (Martin and Geupel 1993). Nest searching occurred daily beginning at approximately 0700 hours until approximately 1400 hours. I searched areas of high nesting activity every 2 days. When a nest failed or fledged the area was checked for re-nests within 2 days. Areas with little or no nesting activity were checked weekly.

Nests were monitored daily during the building stage and when nestlings were visible in the nest (prior to fledging). In order to avoid nest disturbance due to observer effects, adults were not flushed; therefore, nest contents were not examined or touched. Observation of adults on the nest for 2 consecutive days indicated an active nest. During incubation and early nestling stage, when the contents could not be seen from a distance using binoculars, nests were checked every 1–3 days for activity. When nestlings were approximately 6 days old, they were visible through binoculars. A nest was considered to have fledged when the nestlings were ≥10 days, or if fledglings were observed in close proximity of the nest (Bivings 1980). I considered a nest failed if it was empty before nestlings were seen in the nest, and/or if broken eggshells, feathers, or nestling remains were found. Unknown (fate was not determinable) and abandoned nests were not excluded from nest site selection analyses, but were excluded from analyses associated with nest fate.

Nest Aggregations and Spacing

The distance from each nest to its nearest white-winged, mourning, or Inca dove nest was measured and categorized. The neighboring nest had to have been active when incubation of the focal nest was initiated. Cottam and Trefethen (1968) defined a white-winged dove colony as having ≥10 pairs/0.4 ha. This amounts to a maximum radius between nests of 20.2 m. Distances between nests were categorized into ≤20.2 m, 20.3-40.4 m, or >40.5 m.

Vegetation Measurements

Nesting Substrate.—Vegetation measurements were taken after the nest and surrounding nests were inactive to avoid disturbance. Information recorded included the substrate species and circumference. Crown diameter was determined by measuring the distances of the longest and the shortest diameters and then averaging the distances (Bonham 1989). Minimum and maximum canopy heights were measured at the lowest and at the highest points of foliage, respectively. Minimum canopy height below and maximum canopy height above the nest were measured when applicable. Canopy cover was measured with a densiometer at 5 points: 1 below the nest, and 4 taken 1 m from the center of the nest in 4 cardinal directions. Ground cover within 20 m of the focal tree was estimated using a Daubenmire frame (Daubenmire 1959). The location was determined using Skalaski's (1987) algorithm for random sampling in circular plots. The percentage of live vegetation, litter, and bare ground was estimated and ranked from 1–6 according to Daubenmire's method. Additionally, 2 land-cover categories, necessary for ecological urban studies were added (Alberti et al. 2001), concrete/road and structural, which included man-made objects.

Nest Placement Characteristics.—Height of the nest above ground was measured from the bottom of the nest to the ground directly below. The distance from the center of the substrate, usually the tree trunk, to the center point of the nest was measured horizontally. The orientation of the nest from the substrate center was recorded and classified based on the time of day and sun azimuth: (1) morning sun from sunrise until 1200, 63–130°, (2) mid-afternoon from 1200 hours until 1700 hours when the azimuth

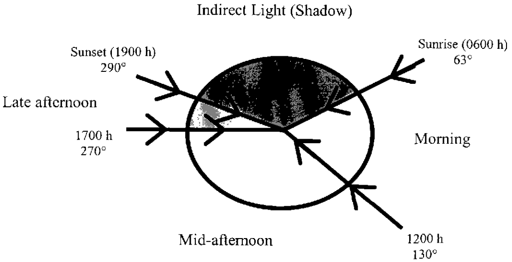

Fig. 3. Diagram of sun azimuth categories for nest orientation classification.

was at a 30° of the horizon, 130–270°, (3) late afternoon from 1700 hours until sunset around 1930 hours, 271–290°, and (4) the angle at which no direct sun is received, termed shadow, 291–62° (Fig. 3). The number of supporting branches was counted and the main branch supporting the nest was classified as horizontal (0–45° from the horizontal) or vertical (45–90°). Distance from nest to nearest lateral foliage edge also was measured.

Random Trees.—Available nesting sites were selected using Universal Transverse Mercator (UTM) coordinates from an aerial map, and then located with a hand held Global Positioning System unit (Magellan 300). All trees ≥3.0 m in height were considered available nesting sites. Vegetation measurements included species, circumference, crown diameter, maximum and minimum tree height, canopy coverage, and ground cover, as described above.

Data Analyses

Nest survival was calculated with incubation intervals of 14 days (Swank 1955, Miller et al. 2001) and nestling period was selected to be 12 days for all species (Swank 1955, Hayslette and Hayslette 1999). Nesting success was estimated using the Mayfield (1975) method and Johnson's (1979) method of reporting 95% confidence intervals. Daily survival for incubation, nestling, and both periods was calculated. Incubation, nestling, and total nesting success (incubation and nestling period combined) were calculated (Mayfield 1975, Johnson 1979). Initiation date was backdated using the incubation and nestling intervals described above for nests in which hatch or fledge days were determined.

To examine tree species preference for nest sites, Johnson's (1980) method of ranking tree availability and use was used. Preference was inferred based on the difference between the use rank and availability rank. Categories included 5 common tree species (American elm, live oak, mesquite, pecan, and silver maple) and the following 3 combined categories of uncommon species: (1) conifers (Pinaceae), (2) oak species (post, water, and Spanish oak), and (3) ornamentals (smaller, flowering trees).

To describe individual selection of nesting trees for each dove species, a 2-sample *t*-test was used to compare characteristics of trees used for nesting relative to randomly selected trees. Variables tested include (1) tree circumference, (2) canopy diameter, (3) tree height, and (4) canopy cover. To examine characteristics of nesting trees among the 3 dove species, a 1-way analysis of variance was used. Additionally, means and 95% simultaneous confidence intervals were constructed. Variables included (1) circumference of nest tree, (2) canopy diameter, (3) nest tree height, (4) canopy cover, (5) ground cover, (6) average distance to closest tree, (7) nest height, (8) distance from nest to center of canopy, and (9) distance from nest to foliage edge. A Chi-square goodness of fit test (Ott 1993) was used to compare (1) distribution of nests in central or rural settings, (2) nest orientation, (3) vertical placement in the canopy, (4) use of horizontal or vertical limbs, and (5) number of supporting branches.

RESULTS

Of 135 total nests located in Mason, Texas, between 1 June and 12 August 2001, 88 (65%) were white-winged, 27 (20%) mourning, and 20 (15%) Inca dove nests. Peak initiation for mourning and Inca doves was during June. White-winged doves had 2 peaks, 1 in June and another in July. Of the nests initiated in June, 72% were successful, while 76% were successful in July. Mourning dove nests initiated in June or July were 50% successful.

Of nests where fate could be determined, the percent nest success was lowest for mourning doves (37%, $n = 27$). White-winged dove nest success was 50% ($n = 78$) and Inca dove nests had the highest percent success 62% ($n = 21$). Mourning doves had the lowest daily nest success rates during all stages, and the lowest incubation, nestling, and nest cycle nest success rates (Table 1*a*). Inca doves had the highest overall nest success during both incubation and nestling period as well as throughout the entire nesting cycle (Table 1*b*). For all 3 dove species, nest success rate was lowest during the incubation stage.

Town Distribution

There was segregation of white-winged and mourning dove nests between peripheral and central locations of Mason, Texas. Almost all (96%) white-winged dove nests were located in the center of town, while 77% of mourning dove nests were located on the edge of town. Inca doves showed less difference between locations (Table 2). White-winged doves had higher percent nest success in the central (59%) location than on the periphery (33%). Conversely, Inca doves had higher percent nest success on the

Table 1*a*. Daily nest success rates (95% CI) using Mayfield (1975) estimates for white-winged, mourning, and Inca doves during incubation and nestling period. Data taken in Mason, Texas from June–August 2001.

Dove species	Number of nests	Incubation[a]	Nestling[b]	Nesting cycle[c]
White-winged dove	61	97.4 (96-98.8)	98.6 (97.6-99.7)	97.3 (96.4-98.2)
Mourning dove	18	93.8 (89.3-98.4)	94.7 (90.8-98.6)	94.7 (91.8-97.6)
Inca dove	16	98.6 (97.5-99.6)	98.7 (95.7-1.02)	98.4 (96.9-99.9)

[a] Based on 14 d incubation period.
[b] Based on 12 d nestling period.
[c] Based on total nesting cycle of 26 d.

Table 1*b*. Nest success (95% CI) using Mayfield (1975) estimates for white-winged, mourning, and Inca doves for nesting cycle. Data taken in Mason, Texas from June–August 2001.

Dove species	Number of nests	Incubation[a]	Nestling[b]	Nesting cycle[c]
White-winged dove	85	69.5 (56.6-85)	84.6 (74.6-95.9)	49.5 (38.9-62.9)
Mourning dove	24	40.9 (20.4-79.2)	52 (31.5-84)	24.2 (10.9-52.5)
Inca dove	17	81.5 (44.6-96.4)	85.2 (59.1-1.2)	65.5 (44.6-96.4)

[a] Based on 14 d incubation period
[b] Based on 12 d nestling period
[c] Based on total nesting cycle of 26 d

Table 2. Location and fate[a] of white-winged, mourning, and Inca dove nests in Mason, Texas, nesting from June August 2001. Study sites were divided into central or peripheral classification based on proximity to residential or commercial locations.

	Nest Fate				
	Success	Fail	Unk[b]	Aband[b]	Total
White-winged Dove					
Central	44	31	7	5	87
Peripheral	1	2	0	1	4
Mourning Dove					
Central	2	3	1	0	6
Peripheral	8	11	2	0	21
Inca Dove					
Central	7	5	0	1	13
Peripheral	6	1	0	1	8

[a] Nest fate analyses include only nests determined as success or fail.

[b] Unk = unknown nest fate, Aband = nest abandoned before laying eggs

periphery (86%) then centrally (58%). Mourning doves had low nesting success across both locations (40% in central and 42% on the periphery; Table 2).

Results from the call counts conducted on 12–14 June 2001, indicate a significant (X^2 = 37.04, df = 2, P = 0.000) difference among dove species and central or peripheral location. More white-winged doves were heard calling in the central portions of town (80%) than mourning (17%) or Inca doves (25%).

Nest Aggregations and Spacing

Of the 79 white-winged dove nests, 35 were within 20.2 m of another nesting white-winged dove, and 45% were successful. Of those white-winged doves that nested 20.3–40.4 m from another active conspecific, nest success was higher with 68% fledging young. White-winged doves that nested >40.4 m from another conspecific nest were most successful with 75% fledging young (Table 3*a*). Mourning doves initiated nesting within 20.2 m of 5 active nests, 3 white-winged doves (2 successful) and 2 conspecifics (1 failed, 1 unknown). Of mourning dove nests initiated within 20.3–40.4 m of another nest, 4 were conspecifics and 50% were successful. Most mourning dove nests were initiated >40.5 m from an active dove nest (Table 3*b*). Of the Inca doves that initiated nesting within 20.2 m of an active dove nest, 2 were white-winged doves and 3 were conspecifics (2 successful). Only 3 initiated nests within 20.3–40.4 m of another active nest and they were all conspecifics (2 failed). The majority of Inca doves (n = 8) initiated nesting >40.4 m from another active nest and 7 (80%) were successful (Table 3*c*).

Table 3*a*. Number, fate, and neighboring species of white-winged dove nests that initiated nesting within the distance categories of another dove species in Mason, Texas, during June–August 2001.

	No. of white-winged dove nests						
	≤ 20.2 m			≤ 40.4m			>40.4 m or none
Nest fate	White-winged dove	Mourning dove	Inca dove	White-winged dove	Mourning dove	Inca dove	
Success	14	1	0	15	0	1	13
Fail	17	0	1	7	0	2	4
Unknown	2	0	0	2	0	0	3
Abandoned	2	0	0	0	2	0	0
Total	35	1	1	24	2	3	20

Table 3*b*. Number, fate, and neighboring species of mourning dove nests that initiated nesting within the distance categories of another dove species in Mason, Texas, during June–August 2001.

	No. of mourning dove nests						
	≤ 20.2 m			≤ 40.4m			>40.4 m or none
Nest fate	White-winged dove	Mourning dove	Inca dove	White-winged dove	Mourning dove	Inca dove	
Success	2	0	0	0	2	0	3
Fail	1	1	0	0	2	0	9
Unknown	0	1	0	0	0	1	3
Abandoned	0	0	0	0	0	0	0
Total	3	2	0	0	4	1	15

Table 3*c*. Number, fate, and neighboring species of Inca dove nests that initiated nesting within the distance categories of another dove species in Mason, Texas, during June–August 2001.

	No. of Inca dove nests						
	≤ 20.2 m			≤ 40.4m			>40.4 m or none
Nest fate	White-winged dove	Mourning dove	Inca dove	White-winged dove	Mourning dove	Inca dove	
Success	1	0	2	0	0	1	7
Fail	1	0	1	0	0	2	1
Abandoned	1	1	0	0	0	0	0
Total	3	1	3	0	0	3	8

Habitat Characteristics

Tree Species.—The dominant tree species in the sample of random trees, were live oak and pecan. White-winged doves used conifers, silver maples, and oak species more than available (Fig. 4). They had no selection preference for live oak and pecan, and used ornamentals, and oak species less than available. White-winged doves had a higher percent of successful nests in pecan (48%), conifers (67%), and silver maple (64%) than in other tree species (Table 4*a*). Mourning doves nested predominately in live oak and did not nest in conifers or silver maple. Mourning doves avoided nesting in oaks, pecans, and ornamentals, showed no preference for mesquite, and preferred American elm and live oak (Fig. 4). For both American elm and live oak, more nests failed (75 and 50%, respectfully) than were successful (Table 4*b*). Inca doves were the most restrictive when selecting tree species; they did not nest in American elm, conifers, mesquite, or ornamental. They selected live oak, silver maple, and oak species, more than available (Fig. 4). Small sample sizes precluded comparison of nest fate for Inca doves. Of the 7 nests in live oak, 57% were successful and of the 7 nests in oak species, 50% were successful (Table 4*c*).

Nesting Substrate Characteristics.—White-winged dove nest trees had larger circumference, canopy diameter, tree height, and greater canopy coverage then random trees. Mourning and Inca doves did not appear to select trees that differed from the available trees based on these 3 of the 4 characteristics. Mourning doves had less canopy coverage than available trees (Table 5). In comparing nest tree characteristics

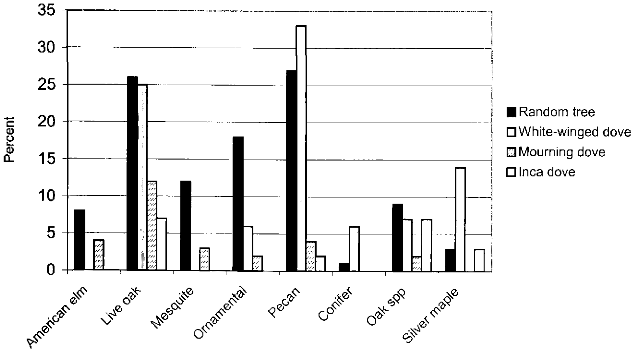

Fig. 4. Percent of tree species in a random sample of available trees in Mason, Texas and percent tree species used for nest substrate by white-winged, mourning, and Inca doves in Mason, Texas, from June–August 2001.

Table 4*a*. White-winged dove nest fate associated with tree species used as nesting substrate in June–August 2001 in Mason, Texas.

Nest fate	Live oak	Ornamental	Pecan	Conifer	Oak spp.	Silver maple
Success	11	3	16	4	3	9
Fail	12	1	11	1	4	4
Unknown	0	1	5	1	0	0
Abandoned	2	1	1	0	0	1
Total	25	6	33	6	7	14

Table 4*b*. Mourning dove nest fate associated with tree species used as nesting substrate in June–August 2001in Mason, Texas.

Nest fate	American Elm	Live Oak	Mesquite	Ornamental	Pecan	Oak spp.
Success	1	5	1	1	2	0
Fail	3	6	1	1	2	1
Unknown	0	1	1	0	0	1
Total	4	12	3	2	4	2

Table 4*c*. Inca dove nest fate associated with tree species[a] used as nesting substrate in June–August 2001 in Mason, Texas.

Nest fate	Live Oak	Pecan	Oak spp.	Silver Maple
Success	4	2	3	2
Fail	2	0	3	1
Abandoned	1	0	1	0
Total	7	2	7	3

[a] Two consecutive Inca dove nests were located on a telephone pole and were excluded from this sample

Table 5. Two-sample t-tests (95% CI) for trees with white-winged, mourning, or Inca dove nests and randomly selected trees in Mason, Texas, from June–August 2001.

	Circumference (m)			Canopy diameter (m)			Tree height (m)			Canopy coverage (%)		
	n	*x*	CI	*n*	*x*	CI	*n*	*x*	CI	*n*	*x*	CI
Random	34	1.43		100	10.29		100	9.95		25	74.6	
White-winged	53	2.09[a]	0.51	75	12.07[b]	1.14	53	12.40[c]	1.11	39	61.0[d]	0.06
Mourning	17	1.27	0.23	21	9.57	1.59	22	9.32	1.17	23	50.6[e]	7.8
Inca	13	1.41	0.36	16	9.29	2.05	18	10.34	1.57	14	57.1	17.0

[a] Significant difference (t = -2.28, p =0.025) between circumference of white-winged dove nest trees and circumference of random trees.
[b] Significant difference (t = -2.38, p =0.018) between canopy diameter of white-winged dove nest trees and canopy diameter of random trees.
[c] Significant difference (t = -3.38, p =0.001) between tree height of white-winged dove nest trees and tree height of random trees.
[d] Significant difference (t = 2.68, p =0.01) between canopy coverage of white-winged dove nest trees and canopy coverage of random trees.
[e] Significant difference (t =-3.68, p =0.001) between canopy coverage of mourning dove nest trees and canopy coverage of random trees.

Table 6. Placement of white-winged, mourning, and Inca dove nests in 4 vertical quadrants of nest tree canopy during June–August 2001 in Mason, Texas.

Vertical Quadrants	White-winged Dove	Mourning Dove	Inca Dove
Top 4th	16	2	0
Mid 3rd	25	2	3
Mid 2nd	21	5	1
Bottom 1st	16	11	21

among the 3 dove species, there were significant differences in all variables except tree circumference (Fig. 5*a*,*b*).

Ground cover was variable among the nest sites (Fig. 6). White-winged doves nested in areas of more live ground cover than both mourning ($t = 3.48$, $df = 2$, $P = 0.000$) and Inca doves ($t = 5.25$, $df = 2$, $P = 0.000$). Mourning doves nested in areas with significantly more litter than Inca ($t = 4.43$, $df = 2$, $P = 0.000$) and white-winged doves ($T = -9.04$, $P = 0.000$). White-winged doves had significantly ($t = 2.43$, $df = 2$, $P = 0.020$) greater ground cover of concrete/road and the structures ($t = 8.68$, $df = 2$, $P = 0.000$) than mourning doves.

Nest Placement Characteristics.— Vertical partitioning of nest sites was different in white-winged dove nest height, and mourning and Inca dove canopy placement. White-winged dove nests were placed significantly ($F = 16.2$, $df = 2$, $P = <0.001$) higher off the ground than mourning and Inca dove nests. There was no difference between mourning ($x = 4.45$, $n = 22$) and Inca dove ($x = 4.44$, $n = 20$) nest height above ground (Fig. 7). Vertical placement in the canopy was significantly different among the 3 dove species ($X^2 = 36.7$, $df = 6$, $P = 0.000$). Mourning ($X^2 = 10.8$, $df = 6$, $P = 0.01$) and Inca doves ($X^2 = 47.16$, $df = 6$, $P = 0.000$) place their nests more often in the bottom fourth of the canopy. White-winged doves placed their nests in the middle portion of the tree more often, however, the differences in nest placement were not significant ($X^2 = 36.7$, $df = 6$, $P = 0.4$; Table 6).

Horizontal partitioning of nest sites was different in nest orientation and distance to foliage edge among the 3 doves. There was a significant ($X^2 = 18.52$, $df = 3$, $P =$

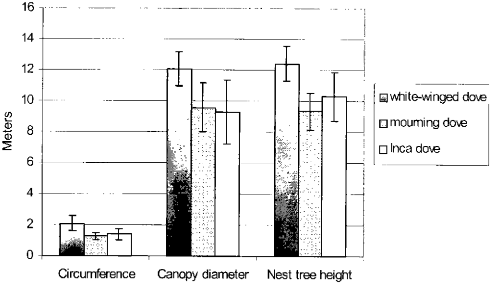

Fig. 5*a*. Nest substrate measurements (95% CI) for nesting white-winged, mourning, and Inca doves in Mason, Texas, from June–August 2001.

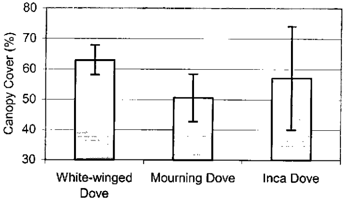

Fig. 5*b*. Nest substrate percent (95% CI) canopy cover for nesting white-winged, mourning, and Inca doves in Mason, Texas, from June–August 2001.

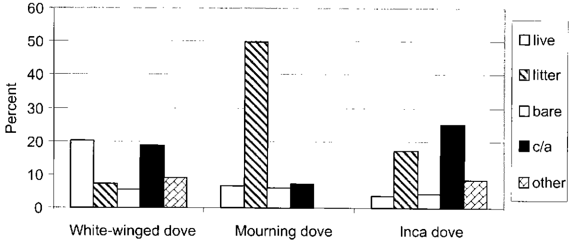

Fig. 6. Percent ground cover within 20 m of active white-winged, mourning, or Inca dove nests in Mason, Texas from June–August 2001.

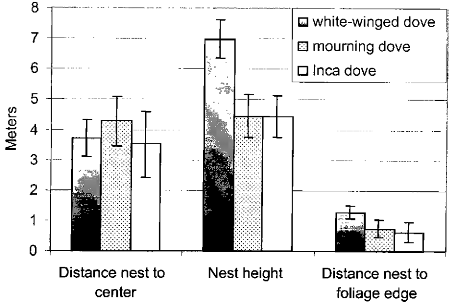

Fig. 7. Nest placement measurements (95% CI) for nesting white-winged, mourning, and Inca doves in Mason, Texas, from June–August 2001.

0.005) difference among and within the 3 dove species for orientation of the nest. White-winged dove nests differed significantly ($X^2 = 28.33$, $df = 3$, $P = 0.000$) in orientation, with 49% ($n = 33$) oriented to the north, which is shaded throughout the day. Slightly fewer nests were oriented towards the mid-afternoon sun, of which 65% were successful. Mourning doves significantly ($X^2 = 15.76$, $df = 3$, $P = 0.001$) oriented nests towards the north, but, there was no difference in nest fates. In contrast, Inca doves significantly ($X^2 = 22.05$, $df = 3$, $P = 0.000$) oriented nests towards the direction of mid-afternoon sunlight of which 67% were successful (Table 7). The distance of nest from foliage edge was significantly different for white-winged doves and mourning doves ($t = 3.11$, $P = 0.03$), as well as for white-winged doves and Inca doves ($t = 3.55$, $P = 0.001$). White-winged doves placed their nests farther in from the edge of the canopy foliage (Fig. 7). The distance from the center of the substrate to the nest was not significantly ($F = 0.57$, $P = 0.566$) different among the 3 dove species (Fig. 7). White-winged ($n = 72$, 92%), mourning ($n = 26$, 100%), and Inca doves ($n = 20$, 90%) used horizontal branches more than vertical and there was no difference between the number of branches used to support their nests.

Table 7. Nest orientation and nest fate of white-winged, mourning, and Inca doves in Mason, Texas during June– August 2001.

	Mourning	Mid-afternoon	Late-afternoon	Shadow
White-winged dove				
Success	7	13	2	17
Fail	2	7	2	11
Mourning dove				
Success	2	0	0	6
Fail	0	2	2	7
Inca dove				
Success	0	8	1	3
Fail	0	4	0	1
Total	11	37	10	51

DISCUSSION

Results indicated some partitioning of nest sites in Mason, Texas, by white-winged, mourning, and Inca doves. The pattern of nest locations suggests, while all 3 dove species are associated with human habitations, white-winged doves are associated with the central areas of Mason, mourning doves were segregated to the peripheral locations, and Inca doves were evenly distributed across both central and rural locations. Conversely, in Tuscon, Arizona, high densities and stable populations of sympatric white-winged, mourning, and Inca doves were found in suburban locations (Emlen 1974, Rosenberg et al. 1987, Mills et al. 1989). Inca doves were found in only suburban areas, whereas white-winged and mourning doves were located in both suburban and riparian areas (Rosenberg et al. 1987). In my study, the low number of mourning dove nests in the center town was unexpected. Mourning doves commonly nest in association with human settlements, such as mature suburbs (Guthrie 1974, Vale and Vale 1976) and college campuses (Swank 1955, Bivings 1980). Additionally, TPW biologists and local residents of Mason, Texas (T. W. Schwertner, TPW, personal communication), observed large numbers of mourning doves in central Mason prior to white-winged dove expansion into the county over the last decade. Inca doves did not appear to differentiate between central or peripheral nesting locations in Mason, Texas. Few studies have been conducted regarding Inca dove habitat use and nesting, although often it is mentioned that Inca doves are highly associated with human settlements (Johnston 1960, Emlen 1974, Quay 1982, Rosenberg et al. 1987, Mills et al. 1989, Mueller 1992). Johnston (1960) described nesting habitat characteristics that explain the high association of Inca doves with suburban environments. Similarly, in this study, both central and peripheral Inca dove nests were associated with human residencies.

In comparison to other mourning dove studies, percent nest success (37%) for mourning doves in Mason was within the range of previous estimates (Caldwell 1964, Yahner 1983), but it was lower than many (Best and Stauffer 1980, Hayslette et al. 2000, Miller et al. 2001). However, Miller et al. (2001) suggested that many studies do not take into account loses as a result of researcher intrusion, therefore, some studies may have underestimated nesting success. Researcher-induced mortality was avoided during this study by maintaining a suitable distance from active nests (Martin and Geupel1993), therefore, nest success results for this study should not be researcher-biased.

In my study, comparing nest success of white-winged doves in central or peripheral locations was not possible because too few nests were located on the periphery. White-winged dove nests in urban areas in south Texas were more successful than those nests in rural locations (Cottam and Trefethen 1968). However, in San Antonio, nest success was lower when compared to results from other studies of white-winged doves in native habitats (West 1993).

Nest Aggregations and Spacing

White-winged doves nesting in Mason displayed both colonial and dispersed nesting strategies. The highest density of white-winged doves was in the residential area. No 2 nests were found active in 1 tree at the same time period, therefore, at the end of the season almost every tree at one point in time had contained a white-winged dove nest. Cottam and Trefethen (1968) reported higher nest success in dispersed nests than in colonial, however, colonial nests still produced more young/unit area because of clumped nest distribution. In my study, more white-winged doves nested within close proximity to conspecifics than not, however, percent nest success increased with distance from conspecific nests. In areas of high nesting density, white-winged doves were gregarious and conspicuous, which could have had 2 primary effects on the results of this study: (1) clumped nests may have been easier to locate than solitary nests, and (2) predators also may have cued in on high nesting densities. Great-tailed grackles (*Quisicalus mexicanus*), the primary nest predator of white-winged doves, prey on nesting colonies. Male white-winged doves nest during the day and will temporarily leave the nest in order to display to intruder males, during which time grackles steal eggs and young (Blankinship 1966).

Mourning doves initiated nesting more often away from other columbids, yet, those that nested near other active nests were more often near conspecific nests. Mourning doves are not known to nest in colonies, although, at high population densities, it is common to see a mourning dove nesting in every tree or several in a tree together (McClure 1942, Swank 1955, Griffin 1994). The relationship between densities of intra- or interspecific nests and nesting success has not been studied for doves. Theory predicts that predation increases with high densities of coexisting species using similar nest sites, thus partitioning of nest sites (Martin 1992, 1993) and increasing distance between active nests (Tinbergen et al. 1967, Page et al. 1983, Lariviere and Messier 1998) should be favored. Therefore, when populations of conspecifics are low, mourning doves may nest allopatrically (Lowe 1956, Griffin 1998). Similarly, mourning doves may avoid nesting near white-winged doves due to the potential for high nest densities of colonial species to attract attention from predators. These predictions also apply to Inca dove nest spacing, however, small sample sizes in this study may have confounded results. Inca doves nests were more aggregated with conspecifics than mourning dove nests, however, those that nested allopatrically from other columbid nests experienced greater nest success.

Interpreting the associations of nest spacing and success in this study were difficult due to small sample sizes. Additionally, the distance categories chosen in this study to examine nearest neighbor effects may not have been large enough to adequately define allopatric and sympatric nests. A study of nest predation on rufous turtle-doves (*Streptopelia orientalis*) on a college campus indicated that neighboring nests effected focal nests <70 m away (Wada 1994).

Nesting Substrate

In my study, white-winged doves selected large, mature trees with dense foliage. Research indicates white-winged doves in urban settings often use live oak, pecan, and ornamentals for nesting substrate (Neff 1940, Cottam and Trefethen 1968, Oberholser 1974, West et al. 1993). The dominance of large pecans and live oaks in Mason may be one of the original reasons why white-winged doves were able to quickly adapt to nesting in Mason. Two sections of town contained high densities of nesting white-winged doves: the school property and a residential area. Live oaks dominated the school playground, in which the original colony of white-winged doves established nest sites. Nests in these trees during my study were mostly unsuccessful (all but 1 of these nests failed early in the nesting stage). Latter this small group of white-winged doves moved towards the school buildings into larger silver maples. The residential area, comprised predominately of large pecan trees and oaks, supported the highest density of white-winged doves on my study sites. Ornamentals, as defined by this study, were usually smaller and less sturdy than the larger pecans and live oaks.

Tree species selection by mourning doves in Mason was similar for locations with high mourning dove densities in Texas, which are often dominated by live oak (Swank 1955, Bivings 1980). Mourning doves also nest in high densities in pecan orchards (Griffin 1994). Their apparent avoidance of pecan trees in Mason may be a result of confounding factors, such as high white-winged dove densities. Several central suburban locations, absent of mourning doves, were dominated by pecan trees, yet, white-winged dove densities were high at these locations. Conversely, 2 rural locations dominated by pecan trees, contained 4 mourning dove nests and no white-winged dove nests. Although mourning doves are considered generalists, selecting for a variety of nesting sites, the crucial feature may be stability of the nest site (Coon et al. 1981). Additionally, Caldwell (1964) suggested that tree species might not be as important as the location of the tree. The abundant ground cover surrounding mourning dove nests was litter (Fig. 10), suggesting a preference for available nest material in close proximity to the nest (Swank 1955). Conversely, the abundance of litter may be an artifact of nest site locations in rural settings. Studies in south Texas have indicated mourning dove preference for mesquite (Passmore 1981, Hayslette et al. 2000). However, in Mason, Texas, very few nests were located in mesquite suggesting mesquite may be a sub-optimal selection when live oaks and pecans are not available for nesting.

In my study, Inca doves appeared to select live oak, deciduous oak species, and silver maples. However, as suggested by Johnston (1960) proximity to open foraging grounds and interspersed tall vegetation for nesting, cover, and roosting may be important for Inca dove nest sites, as opposed to nest substrate species. A telephone pole in Mason, Texas provided a pair of Inca doves with the necessary nesting substrate for 2 successful broods.

There was considerable overlap among white-winged, mourning, and Inca doves for selection of live oak for nesting substrate. As opposed to other tree species in Texas, live oaks retain their leaves year-round thus providing cover for nest sites. Additionally, live oaks have sturdy horizontal branches and clumped leaf foliage at the primary branches (Swank 1955). Due to extended breeding seasons, mourning and Inca doves may rely on live oak to provide nest sites when other trees have dropped their leaves; however, during peak breeding season, when all trees are foliated, both doves will use other tree species (Swank 1955). Urbanization provides an environment conducive for avian species to expand their breeding season (Schoech 1996, Marzluff 1998), and residential white-winged doves in urban environments may initiate breeding earlier (West 1993). This increase may lead to competition for live oaks early in the season, however, my study was not initiated until June, and thereby not addressing this possibility. Further research should examine this overlap in resource use by all 3 dove species.

Nest-Site Partitioning

Vertical partitioning of nest sites in the canopy of the tree may benefit mourning and Inca doves. White-winged doves nested higher off the ground than mourning or Inca doves, yet did not select for any vertical placement in the canopy. Mourning and Inca doves nested primarily in the lower fourth of the canopy. Predation rates may increase with height of nesting substrate (Caccamise 1977, Yahner 1983, Wada 1994, Reitsma and Whelan2000). Non-columbid species, such as blue jays (*Cyanocitta cristata*) or American robins (*Turdus migratorius*), may displace mourning doves from optimal nest placement towards the lower portion of the canopy when other tree-nesting species are present (Yahner 1983, Griffin 1998). However, white-winged doves showed a slight preference for the center of the canopy, thus any displacement would result in mourning or Inca doves nesting at the base of the canopy, which may be considered an optimal location in the tree.

Horizontal placement of dove nests in the canopy differs among the 3 dove species, specifically in the side of the tree selected for nesting and the distance from the foliage edge. White-winged doves in my study preferred nesting farther in from the foliage edge than mourning or Inca doves. Griffin (1998) reports an increase in distance of mourning dove nests from the center of the canopy when blue jays are abundant and suggested that this may be a function of partitioning their nest sites from blue jays, which prefer nesting in the central portion of the canopy.

Dove nests were horizontally partitioned by orientation of the nest from the substrate that probably results from physiological requirements of the individual dove species as opposed to pressure from nest site use of coexisting species. Average temperatures in Mason, Texas, during the summer months reach extreme limits. White-winged dove nestlings in the LRGV were observed to be highly susceptible to over-heating should the adult be flushed from the nest (Cottam and Trefethen 1968). This study indicated that white-winged and mourning doves might be selecting the side of the trees that receives indirect sunlight through out the day (approximately north). Although, a large percentage of white-winged doves nested where they receive the direct mid-afternoon sun (approximately southeast, south and west), this may be ameliorated by white-winged doves selecting nesting trees with more canopy coverage than what is available and by placing their nest away from the foliage edge. Mourning doves placed nests in order to avoid the mid-afternoon sunlight. Orientation may be a critical factor in nest placement since they may place their nests farther out from the center of the canopy. Yahner (1983) found the majority of mourning dove nests in Minnesota oriented towards the south and east and suggested this as a means of avoiding summer storms that approach from the north. Inca doves, which are sensitive to cold temperatures (Mueller 1992), are known to place nests in direct sunlight (Johnston 1960). In my study, they oriented their nests towards the mid-afternoon sun (south) the majority of the time. The smaller size of the Inca dove may dissipate heat quicker than the larger doves, thus requiring additional warmth from environmental factors.

Niche Overlap and Competition

Inca and mourning doves did not appear to partition their nest sites in this study. Inca doves are of a different genus, and therefore, may differ ecologically in ways unexamined in my study. For example, Inca doves are smaller than white-winged and mourning doves and they have a scaled pattern on their back and wings. Their small size, elusive behavior, and coloration may help conceal an adult on a nest. Additionally, they may place their nests in different locations not identified by the characteristics measured during this study. The small sample size of Inca dove nests in this study may be researcher-biased in that their nests were more difficult to find by strategic searching than the other 2 dove species, although all Inca doves located on study sites were monitored for nesting behavior.

Ecologically similar species, such as white-winged and mourning doves, should theoretically partition some niche dimension in order to coexist and reduce competition (Cody 1974, Pianka 1978, Wiens 1989*a*). Of the 3 primary niche dimensions, time, diet, and space (Schoener 1974), there is no temporal differentiation in resource use for columbids; all species are diurnal and breeding seasons overlap for at least 3 months during the year. Additionally, urban columbids rely heavily on supplemental food thus increasing dietary resource overlap to a level where competition for food may be inconsequential. Preemptive competition (Wiens 1989*b*), the remaining niche dimension, may be a critical selection pressure on nest site acquisition and nest success for doves in urban environments. Within an urban ecosystem, as a result of increased avian densities (Beissinger and Osborne 1982) and habitat fragmentation (Blair 1996), available habitat is decreased by: (1) reduced vegetation in low, middle, and canopy layers (Beissinger and Osborne 1982), (2) increase in nest predators, (3) increase in disease, parasites, and environmental contaminants (Pierotti and Annett 2001), (4) increase in intra- and interspecific competition, and (5) increase in nesting density (Marzluff 2001). Despite limitations to nesting sites, some native birds respond positively to the abundance of resources associated with human settlements (Mills et al. 1989, Blair 1996, Marzluff 2001).

Are urban centers optimal habitat for white-winged, mourning, and Inca doves? If white-winged doves are excluding mourning and Inca doves from urban centers, and if urban ecosystems are optimal habitat for mourning and Inca doves, then concern arises over whether rural, or less suitable habitat, will sustain populations of mourning and Inca doves. Columbids are highly adaptable (Goodwin 1983, Baskett and Sayre 1993) and because of their physiological and behavioral requirements, they benefit from human induced alterations. Their reproductive strategy allows for production of multiple broods over one season (Westmoreland et al. 1986, Blockstein 1989), thus promoting a stable and often dense population, characteristic of urban populations (Emlen 1974, Marzluff et al. 1998). Factors associated with urbanization that promote preferential selection by doves include supplemental food and water, habitat requirements, and open suburban lawns for foraging. Supplemental food and water, supplied by feeders and birdbaths, may increase survival and reproductive fitness (Brittingham and Temple 1988).

Human environments have heavy water demands resulting in increased standing water in which urban birds directly benefit (Marzluff 1998). Inca doves must meet rigid water requirements and may be reliant upon readily available water associated with human settlements (MacMillian and Trost 1966). Intermediate development, such as parks, golf courses, and residential areas, are characterized by ornamental or shade trees interspersed among open lawns or grassland areas. Lawns are of greater live vegetative biomass than natural grasslands providing a concentrated food supply. Additionally, open lawns provide ample space for bird flocks and predator visibility is unobscured (Falk 1976). Mourning doves avoid heavy vegetation that interferes with their ability to detect predators and foraging efficiency is reduced because they visually search for seeds without probing or scratching the ground (Davison and Sullivan 1963, Lewis 1993).

The possibility exists that some other factor is responsible for the exclusion of mourning doves to the periphery of Mason, Texas. Competitive exclusion of a species by a dominant species is often attained by direct physical aggression (Wiens 1989*a*, Martin and Martin 2001*a*), however no physical aggression was witnessed among the 3 dove species in Mason. There were 2 occasions in which white-winged doves demonstrated direct dominance behavior, both occurred during nest material acquisition. A white-winged dove stole nest material directly from underneath an adult Inca dove nesting on a telephone pole while the Inca dove's mate perched next to the nest. Neither Inca dove responded to the white-winged. The second occurrence was when 2 white-winged doves were collecting material in a street and a mourning dove landed nearby. The white-winged doves both aggressively approached the mourning dove who quickly vacated the area and the white-winged doves proceeded to display to each other until one retreated to its original spot a few meters away.

This study was limited to 1 year, therefore, yearly effects can not be ruled out. Other factors to be included in future research should include indirect effects of white-winged dove densities in town such as increase in diseases or parasites, such as *Trichomonas gallinae* (Conti and Forrester 1981, Conti et al. 1985, Glass et al. 2001). Additionally, other habitat parameters should be examined as well as habitat alterations, such as maturation of trees in center locations of Mason may no longer be preferable to mourning or Inca doves. Interactions with species other than columbids should be addressed.

Mourning doves show considerable plasticity in nest-site selection and use of tree species. Despite this, their population has been decreasing (George et al. 2001). This decline may be a result of habitat loss in their native woodlands, or competition with increasing populations of more aggressive species. Determining the competitive effects of white-winged doves on coexisting columbids would require several years of information on a nesting population of doves prior to the expansion of white-winged doves into their urban habitat. As urbanization and habitat destruction increases, white-winged, mourning, and Inca doves may become more reliant upon human settlements for resource acquisition, thus necessitating a more thorough understanding of interspecific competition amongst urban nesting avian species.

SUMMARY AND IMPLICATIONS

This study, conducted in Mason, Texas, from June-August 2001, identified the following results and implications for future research in order to evaluate the impact of expanding white-winged dove populations into urban environments on mourning and Inca dove populations.

1. White-winged and mourning doves spatially segregated their nests across town, with white-winged doves nesting in the center and mourning doves nesting on the periphery.
2. Mourning doves experienced low nest success in central and peripheral locations, whereas Inca doves had the highest nest success for all locations.
3. All 3 dove species initiated nesting near conspecifics more often than interspecific nests. White-winged doves indicated both colonial and solitary nesting, with nest success increasing with distance from a conspecific nest.
4. All 3 dove species preferred live oak as a nesting substrate. Additionally, white-winged doves also preferred mature pecan trees and Inca doves also preferred oaks.
5. White-winged doves preferred taller, larger mature trees for nesting. Mourning and Inca doves preferred nest substrates based on tree circumference, canopy diameter, and height. Mourning doves preferred trees with less canopy cover than random trees.
6. There was some nest-site partitioning among the 3 doves. White-winged doves nested higher off the ground than mourning or Inca doves, but nested vertically

throughout the canopy. Mourning and Inca doves nested in the lower quartile of the canopy. Nests were horizontally segregated in the canopy by white-winged doves nesting farther in from the foliage edge than mourning or Inca doves. Inca doves oriented their nests to the southeast, south, and southwest sides of the tree canopies, whereas mourning doves oriented their nests to the northwest, north, and northeast sides. Nest-site orientation for white-winged doves overlapped with both mourning and Inca dove nest orientations.

7. It is imperative to obtain nesting data on mourning and Inca doves in locations prior to the expansion of white-winged doves into the area. Additionally, with increasing urbanization and white-winged dove population expansion, an understanding of the effects of urban environments on dove production is needed.

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Research Interests:

Avian breeding ecology, physiology, behavior, and life histories; wetland ecology; wildlife management