FINAL REPORT

BANDING TO MONITOR SURVIVAL AND HARVEST OF WHITE-WINGED DOVES IN TEXAS

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MOURNING DOVE BANDING IN TEXAS

Report to:

Texas Parks and Wildlife Department

21 November 2011

Investigator:

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Corey Mason,
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Dear Corey,

Herein contains the final report, detailed as 3 manuscript-style publications, which outlines the results from the banding efforts towards white-winged doves conducted by Texas A&M University between 2006 and 2010. Since 2006, Texas A&M University, in conjunction with Texas Parks and Wildlife has focused on the initial development and implementation of a white-winged dove banding program in Texas in support of future long-term management actions. The focus of the banding program, now completed, was to band white-winged doves across the state of Texas such that valid inferences can be made regarding survival, recruitment, and harvest of white-winged doves as they have recently expanded their range in Texas.

Contained within this final report are 3 individual reports:

- Distribution and derivation of white-winged dove harvests in Texas
- Survival, fidelity, and recovery rates of white-winged doves in Texas
- Immigration and recruitment in an urban white-winged dove breeding colony

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Distribution and Derivation of White-winged Dove Harvests in Texas

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KEY WORDS band-recovery, fidelity, harvest derivation, migration, spatial distribution, Texas, white-winged dove, *Zenaida asiatica.*

ABSTRACT Band-recoveries provide requisite data for evaluating the spatial distribution of harvest relative to the distribution of the breeding stocks for a wide variety of migratory species. We used direct and indirect band recovery data to evaluate the distribution and derivation of harvest of white-winged doves (*Zenaida asiatica*) banded pre-season in 3 distinct strata in Texas during 2007-2010. We banded 60,742 white-winged doves during 2007-2010 and based on 2,458 harvest recoveries, majority (>95%) of white-winged dove harvest occurred during the first 2 months of season (Sept-Oct). Juvenile white-winged doves represented a greater percentage of the direct recoveries than adults across all strata (north=80%, central=69%, south=82%) and the majority of direct band recoveries (north=75%, central=90%, south=78%) occurred within the original banding strata. Age-specific weighting factors and harvest derivation indicated that both juvenile and adult harvest was highest within the strata of original banding. Harvest distribution data corrected for band reporting rates indicated high fidelity of white-winged doves to specific geographic strata, with little interplay between strata. Our results suggest that population vital rate estimates for survival and harvest for use in future Adaptive Harvest Management should focus on stock-specific levels.

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The white-winged dove (*Zenaida asiatica*) is a widely-distributed dove species within the southwestern U.S. and Mexico (George et al. 1994) with populations introduced in Florida in the late 1970s (Schwertner et al. 2002). Historically confined to semi-arid and arid habitats in the southwestern U.S. and Mexico, white-winged doves have slowly expanded into a variety of environments across the southwestern U.S (George et al. 1994). Outside of their historic thorn-scrub habitats in the Lower Rio Grande Valley (Cottam and Trefethen 1968, George et al. 1994) white-winged dove breeding colonies in Texas are found primarily in urban environments (Schwertner and Johnson 2005). As white-winged dove populations continue expansion to the north throughout the southwestern range (Veech et al. 2011), it is important to identify changes in white-winged dove distribution as regulatory and management decisions must account for geographic shifts in breeding populations and the potential impacts on harvest distributions and species demography (Munro and Kimball 1982, Sheaffer and Malecki 1996, Royle and Dubovsky 2001).

Although limited in distribution, white-winged doves are second only to mourning doves in terms of total harvest of webless migratory game birds (≈1.6 million total annual harvest nationwide with ≈1.3 million harvested in Texas; Raftovich et al. 2010). Within their known range, population trajectories are variable, with historical strongholds like Arizona (George et al. 1994) showing long-term declines in breeding dove surveys (Pacific Flyway Council 2003, Rabe and Sanders 2010) while expansion in both white-winged dove distribution (Veech eta l. 2011) and harvest (Raftovich et al. 2010) has occurred in Texas. Concomitant with expansion, white-winged doves have experienced changes in habitat selection, migration phenology, regional fidelity, and harvest distribution (Schwertner et al. 2002, Schwertner and Johnson 2005, Rabe and Sanders 2010). Previous analysis of banding data (George et al. 2000) contributed to our knowledge of species demography; however those data were collected 40 years ago in the historic species range pre-expansion (Cottam and Trefethen 1968, Schwertner et al. 2002) and thus likely do not provide a representative evaluation of current population status. Additionally, updated spatial distribution of harvested white-winged provides insights into geographical stratification of breeding (stock) populations available for harvest and thus has implications for ongoing regulatory planning and management (Otis et al. 2008).

To date there has been no focus on evaluating harvest distribution, derivation, or other population parameters requisite for supporting rangewide management planning for white-winged doves even though population distribution data is necessary for development of Adaptive Harvest Management strategies (Munro and Kimball 1982, Johnson and Moore 1995, Williams and Johnson 1995, Conroy et al. 2002). Because accurate spatial stratification can reduce uncertainty in demographic parameters and increase accuracy of model predictions (Otis 2004, Zimpfer and Conroy 2006) and because >80% of the annual harvest of white-winged doves occurs in Texas (Raftovich et al. 2010), our focus was to 1) evaluate and update information on the distribution of harvest of white-winged doves banded in Texas and the derivation of doves harvested in Texas, 2) compare distribution of recoveries based on banding conducted within the historic south Texas range pre-expansion to current distribution and recovery locations of white-winged doves banded within the south Texas range post-expansion to evaluate whether harvest distribution is changing over time, and 3) determine whether distinct trends in extent, recovery direction, and population distribution exist for better informing management actions and regulatory timing.

METHODS

We compiled records of white-winged doves banded pre-season across Texas during March-August from 2007-2010 (n = 60,742) as part of a larger white-winged dove population ecology study. Banding efforts within geographic strata were distributed proportional to white-winged dove density based on Texas Parks and Wildlife survey data and historic banding records. When captured, all birds were aged into hatch year (HY) and after hatch year(AHY) based on gross morphological characteristics (Cottam and Trefethen 1968) and banded with U.S. Fish and Wildlife Service (USFWS)/U.S. Geological Survey (USGS) size 4 metal bands (2007 used toll free bands, 2008-2010 used both toll-free and web-address bands in an approximate 50:50 split concurrent with the USFWS shifting to a web-address return option; Sanders and Otis, In Press). A majority (>95%) of our banding effort was focused on white-winged doves in urban environments as dense breeding colonies have moved to urban environments over the last 20 years as availability of native habitats have declined (George et al. 1994, 2000, Veech et al. 2011). We obtained band recovery records (n = 2,458) from the U.S. Geological Survey Bird Banding Laboratory (USGS-BBL) and we used data on recoveries of all banded individuals killed, retrieved, and reported by hunters in a known location with a known age. As dove season in Texas overlaps 2 calendar years, we designated each hunting season by the year in which it began (e.g., 2007 hunting season begins 1 September 2007 and ends in Jan/Feb 2008) and we note that during our study November was closed for dove hunting across Texas. Each recovery was characterized by date of recovery and spatial coordinates (to the southeast corner of the 10' block in which harvest occurred) which provides both temporal and spatial information on the distribution of white-winged doves harvested in Texas each year. For each recovery, we converted locations from the southeast corner to the centroid of the 10' blocks. For a descriptive comparison to historic band recovery data, we compiled records of white-winged doves banded pre-season across Texas during 1950 to 1978 (n = 66,629; George et al. 2000) from the USGS-BBL as well as data on recoveries of all banded individuals killed, retrieved, and reported by hunters in a known location during 1951 to 1980 (n = 5,639) and applied the same methods described above.

During the course of our study, Texas had 3 dove hunting zones and based on these data we created 3 strata approximating these hunting zones (Figure 1). Texas dove hunting zones are typically separated by recognizable boundaries (e.g., interstate highways) simplifying hunter interpretation of hunting zones, but as these are political boundaries which can be easily adjusted, we used the 10 minute latitude closest to each boundary on its western edge to designate strata (north, central, south) for our study. We categorized capture locations for white-winged doves in Texas into specific strata (Figure 1) for distribution and harvest derivation analysis and used the same geographic strata for all capture and recovery data for this study. We calculated age-specific, strata-specific harvest distribution (%) using direct recoveries from white-winged doves adjusted for reporting rate (Munro and Kimball 1982, Otis et al. 2008). We used estimates of reporting rates for mourning doves (Sanders and Otis, In Press) as no reporting rate information is available for white-winged doves and we assumed that reporting rates were constant across strata. We evaluated harvest derivation between and among strata adjusted for population weighting following Kiel (1959), Dunks (1977), Dunks et al. (1982), Munro and Kimball (1982) and Otis et al. (2008). For each strata, we estimated area (north = 26.2 million ha, central = 33.9 million ha, south=8.5 million ha) and used Texas Parks and Wildlife white-winged dove survey data (unpublished) to estimate average white-winged dove breeding density for each strata during our study period (2007-2010) for harvest derivation (Kiel 1959, Dunks 1977, Dunks et al. 1982, Munro and Kimball 1982). We calculated the number and proportion of white-winged doves harvested in each strata relative to all individuals banded in Texas. In addition, we compared direct recovery distribution of white-winged doves banded in our south strata (historical habitats; George et al. 1994) to band recovery data conducted before white-winged dove expansion had begun in earnest (George et al. 2000). We used one-way analysis of variance to evaluate whether average distance from banding to harvest location differed between strata and we created rose-diagram plots to evaluate the circular distribution of band recoveries relative to banding locations between strata across years.

RESULTS

We captured and banded 60,742 white-winged doves between 2007 and 2010 in Texas. We banded 7,098 in the northern strata; 20,300 in the central strata; and 33,344 in the southern strata. We did not have accurate age information on 96, 441, and 140 individuals in the northern, central, and southern strata, respectively, thus we removed those individuals from any age-specific analyses. Recovery data (both direct and indirect) for white-winged doves harvested in 2008-2010 consisted of 873 web-address recoveries and 1107 toll-free recoveries. The proportion of web-address direct recoveries (*n* = 680) (number web-address direct recoveries/total direct recoveries) were consistent each year (2008=41%, 2009=49%, 2010=47%). Juvenile white-winged doves represented a greater percentage of the direct recoveries than adults across all strata (north=80%, central=69%, south=82%). Overall, harvest of white-winged doves primarily occurred during the first 2 months of season (Sept-Oct), with ≤3% (57 of 1,801) of direct recoveries occurring after 1 November (Figure 2). Direct recoveries of Texas banded white-winged doves in United States locations outside of Texas were low, with the north and central strata having only 6 and 9 individual harvested outside of Texas, respectively. The south strata had no recoveries outside of Texas within the United States, but had 97 direct recoveries in Mexico (which for analysis was included in the south strata) during our study period, relative to only 1 and 7 direct recoveries in Mexico from the north and central strata, respectively. Overall, we saw no clear evidence of unique migratory directionality based on our harvest distribution data either between strata or across years (Figure 3). Using our 2007-2010 recovery data, analysis of variance indicated that the mean distance between capture and recovery differed between capture strata, and while did not detect any differences between years with mean distance between banding and recovery locations for white-winged doves in the central strata showing less mean annual variation than the north and southern strata (Table 2), considerable variability of movements within and between strata preclude any specific inferences about temporal changes.

We based harvest distribution analysis (%) using direct recoveries adjusted for band reporting rates. We used band reporting rates for toll-free (0.407) and web-address (0.440) bands (Sanders and Otis, In Press) and assumed no differences in reporting rate between HY and AHY individuals (Table 3). Additionally, we compared harvest distribution of white-winged doves banded between 1950 and 1978 (George et al. 2000) and doves banded between 2007 and 2010. Biologists banded 60,356 white-winged doves in the south strata of Texas during the historic banding efforts, whereas we banded 33,344 white-winged doves during 2007-2010. In general, the distribution of direct recoveries were similar between historic (n = 5,678 direct recoveries over 28 years) and current (n = 1,018 direct recoveries over 4 years) banding with the exception being a noticeable cluster of 432 recoveries in Costa Rica, Guatemala, El Salvador, Nicaragua, and Honduras during the historic banding period compared to only 10 from current banding efforts (Figure 4).

A majority of recoveries within each recovery strata originated from birds banded within those strata (Table 1, Figure 5). Across all strata, the majority (north=75%, central=90%, south=78%) of direct band recoveries occurred within the original banding strata (Table 1), as did the majority of indirect recoveries (north=73%, central=96%, south=75%). Age-specific weighting factors (Table 4) and harvest derivation estimates indicated that both juvenile and adult harvest was highest within the strata of original banding (Table 5). For example, of the total number of white-winged doves harvested in recovery region 1 (banding strata A), that derivation of harvest estimates weighted for population size indicated that 54% of the juveniles and 57% of the adults originated from that banding stratum (Table 5). Banding strata B was the primary source for harvested white-winged doves outside the original banding strata, and banding strata A and C provided little to no birds to each other (Table 1 and 5).

DISCUSSION

Our results indicate that white-winged doves in Texas exist in distinct breeding aggregations with only limited harvest interplay over the north-south gradient. Our harvest distribution and derivation estimates show that white-winged dove harvest within each stratum was supported by those white-winged doves captured or recruited within those strata. Our estimates of regional fidelity were similar, but slightly lower than estimates for mourning doves at the state scale (Dunks et al. 1982, Otis et al 2008). Our results suggest that population vital rate estimates for survival and harvest (Otis 2002) for use in future AHM models should be evaluated at similar stock-specific levels, approximately concordant with the strata used in our research or perhaps by combining non-traditional (north and central) strata into 1 zone and treating the historical range (southern strata) as a separate zone. The most comprehensive analysis of white-winged dove demography to date (George et al. 2000) used only individuals banded in the historic Texas range and Mexico as expansion had not begun in earnest at that time. If other white-winged populations, which are both expanding and contracting in certain areas of New Mexico, Arizona, and California (Rabe and Sanders 2010) are shown to exhibit similar geographic stratification, then future regulatory activities could benefit by evaluating management options and population demography at a stock-specific scale (Johnson and Moore 1995, Sæther et al. 2008) as management of individual stocks with limited interactions can reduce system complexity and simplify long-term management actions (Conroy et al. 2002).

Based on our comparison of historic and current recovery data for the southern strata, we found little evidence that white-winged doves within the historic range have exhibited any significant changes in harvest or migratory patterns between our two study periods (George et al. 2000). However, we suggest that simultaneous to the expansion of white-winged doves is an increasing likelihood of year-round residency and decrease in migration of birds moving south during the annual cycle. Increased residency and reduced migratory activities may have been indicated by our evaluation of mean distances and direction between banding and harvest location as distances showed minimal movements between strata both within and between seasons and migration directionality based on recovery data (Dunks et al. 1982, Munro and Kimball 1982) was approximately uniform across our study strata. Strong inferences regarding migration patterns requires more detailed information than can be provided by band recoveries thus our hypotheses represents an area of additional research need for white-winged doves. However, our analysis of indirect recoveries also supports our hypothesis of increased residency and regional fidelity as a majority of indirect recoveries (n = 657) of white-winged doves were faithful to original banding strata with 73%, 96%, and 93% of white-winged doves banded in banding strata A, B, or C, respectively, being harvested in recovery strata A, B, or C, respectively. We note our results were based on band recovery data and could potentially be influenced by non-uniformity of dove hunting activities across the annual cycle. Dove hunting is primarily an early season recreational pursuit, with other species such as white-tailed deer and waterfowl typically taking precedence in Texas by early November and continuing through January. Thus, lower numbers of recoveries later in the season, on which estimates of migratory patterns and timing would be based (Munro and Kimball 1982), could be influenced by reduced hunting pressure on doves as seasons progress.

The typical definition of harvest distribution is the distribution of harvest (band recoveries) corrected for band reporting rate (Munro and Kimball 1982). Band reporting rates for mourning doves have only recently been estimated across the range (Otis et al. 2008) with Texas band reporting rate estimated between 0.407 (SE = 0.087) and 0.440 (SE = 0.095) (Sanders and Otis, In Press). Currently, estimates exist for white-winged doves as band-reporting studies have not been conducted at a rangewide scale. However, as our work was focused strictly in Texas, we would expect less variation in reporting rates than those found at the flyway or breeding references areas (Munro and Kimball 1982, Otis 2004, Sanders and Otis, In Press) thus we assume that reporting rates should be constant within our study area and therefore we provided harvest distribution estimates corrected for variation in reporting rates for mourning doves in Texas and suggest that future efforts to address reporting rates be incorporated into management planning.

The information on direct and indirect recoveries herein also provides insights into the distribution of hunting effort across Texas. The majority of urban environments in Texas are located along the Interstate-Highway 35 (I35) corridor running north-south through approximately the center of the state. The area within this 100 km buffer of I-35 represents 23% of the total Texas land base and based on the distribution of harvest, 38% of the total harvest based on both direct and indirect recoveries is occurring within 100 km of the I-35 corridor beginning at the Oklahoma-Texas state line and ending at the Texas-Mexico international border. As Texas Parks and Wildlife operates a hunt-lease program wherein the agency leases private lands for public hunting access, our results indicate that if maximizing public hunting opportunities for white-winged doves is of interest, efforts to lease lands along the I-35 corridor and the surrounding urban-rural interface would likely benefit a wide range of hunters (Schulz et al. 2003).

Based on our results, collection of empirical data to evaluate population distribution, demography and harvest derivation across the species southwestern United States range is paramount if AHM, or alternative options (e.g., surplus production) are to be used to drive harvest management of white-winged doves across their range. Our results provide an initial step for identifying spatial variation in white-winged dove populations which may affect vital rates and thus should provide the foundation for further exploration of managing stocks uniquely. Further, if rangewide white-winged dove populations exhibit similar spatial structuring at the state or regional scale, this information should underlie development of modeling frameworks on which to base population management decisions (Johnson and Moore 1995).

MANAGEMENT IMPLICATIONS

Our study identifies distinct stocks of white-winged doves in Texas, and as such we recommend initiation of a regional banding program in Texas, New Mexico, Arizona, and California as these are the four states with substantial white-winged dove populations within the continental United States. Furthering our understanding white-winged dove stocks will assist in development of a modeling framework on which to base regulatory management decisions distinct from that currently proposed for mourning doves (Otis 2004, Otis 2006, Otis et al. 2008). Additionally, as significant breeding populations and harvest opportunities of white-winged doves occur across Mexico, we recommend that future efforts attempt to integrate white-winged dove population management in Mexico into a combined bi-national regulatory framework.

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List of Figures:

Table 1. Distribution of direct and indirect band recoveries of white-winged doves banded (n = 60,742) in Texas, USA during 2007 through 2010 cross-categorized by banding and recovery strata (A=North, B=Central, C=South).

	Recovery Strata			Total Direct Recoveries	Recovery Strata			Total Indirect Recoveries
Banding Strata	A	B	C		A	B	C	
A	128	40	1	169	38	13	1	52
B	19	504	30	553	2	149	4	155
C	2	85	992	1079	0	30	420	450

Table 2. Mean (SD) distance (km) from capture location to direct recovery 10' block centroid for white-winged doves banded in Texas, USA during 2007 through 2010 categorized by banding (A=North, B=Central, C=South) strata.

Strata	2007	2008	2009	2010
A	77 (141)	123 (169)	82 (108)	158 (272)
B	65 (72)	90 (155)	84 (219)	57 (80)
C	92 (169)	110 (239)	86 (216)	87 (243)

Table 3. Percent distribution of hatch year and after hatch year white-winged dove harvest from banding strata to harvest strata within Texas based on direct recoveries from pre-season bandings conducted during 2007-2010. Values represent adjusted counts based on band reporting rates for web-address (0.440) and toll-free (0.407) band types based on Sanders and Otis (In Press) and percentages are relative to the total harvest for each band type.

		Age-specific recoveries corrected for band-type reporting rates (*n* (%))			
		Toll-free		Web-address	
Banding Strata	Recovery Strata	HY	AHY[a]	HY	AHY[a]
A	A	109 (7.0)	22 (1.4)	130 (4.6)	42 (1.5)
	B	36 (2.3)	5 (0.3)	44 (1.5)	10 (0.4)
	C	2 (0.1)	0 (0)	0 (0)	0 (0)
B	A	14 (0.9)	7 (0.5)	20 (0.7)	5 (0.2)
	B	282 (18.2)	134 (8.6)	548 (19.8)	241 (8.6)
	C	30 (2.0)	11 (0.7)	25 (0.9)	5 (0.2)
C	A	2 (0.1)	0 (0)	2 (0.7)	0 (0)
	B	66 (4.3)	16 (1.0)	96 (3.5)	25 (0.9)
	C	634 (41.0)	179 (11.6)	1211 (44.0)	346 (12.5)

[a]Any birds with unknown age were considered AHY in the appropriate band type column.

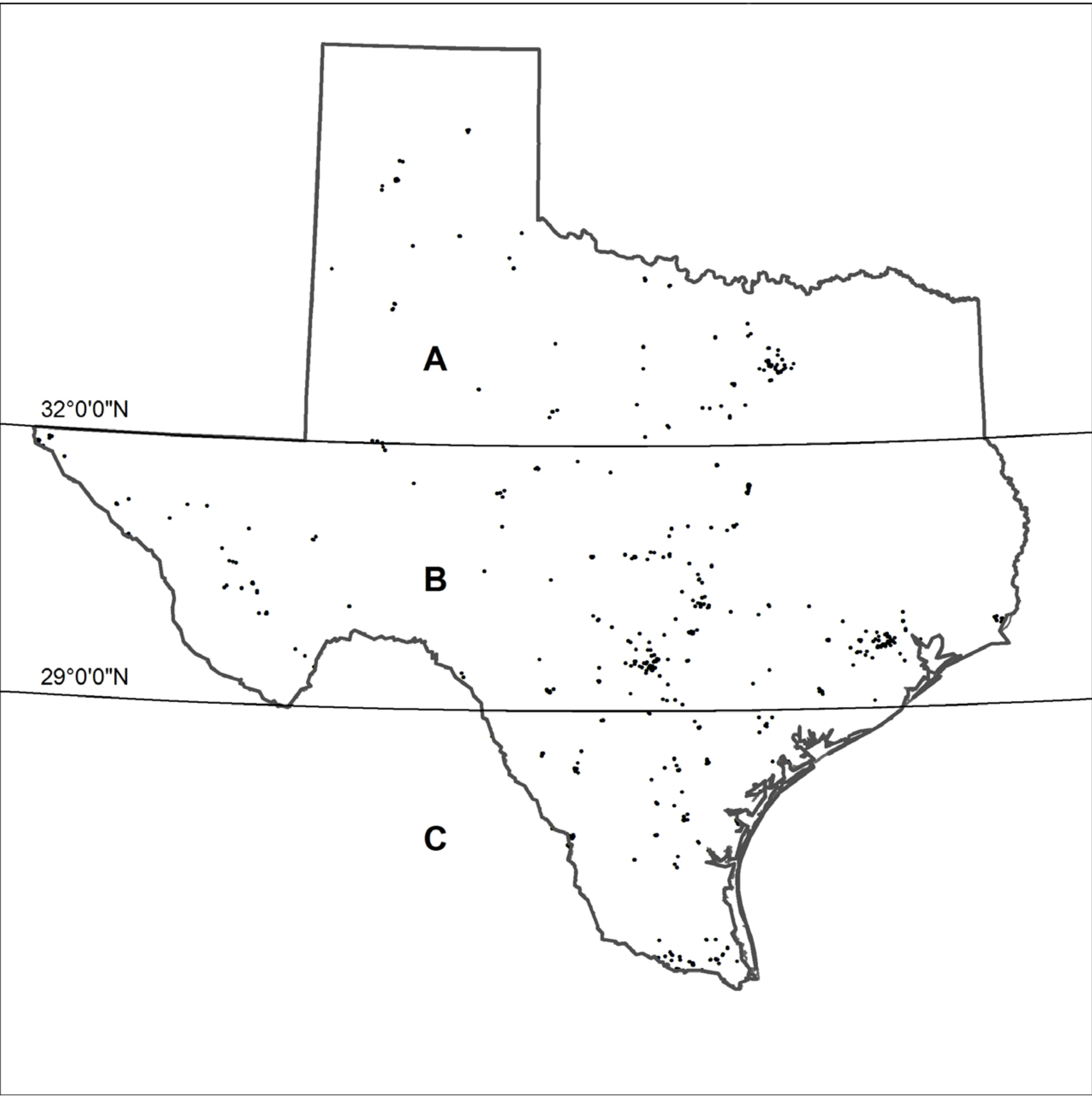
Table 4. Age-specific weighting factors (w_i; J=juveniles, A=adults, T=total) for recoveries of white-winged doves banded pre-season in Texas, USA during 2007 thru 2010. Mean breeding density was based on point count surveys conducted during 2008-2010 by Texas Parks and Wildlife and represent the average number of white-winged doves visually observer per point count survey location.

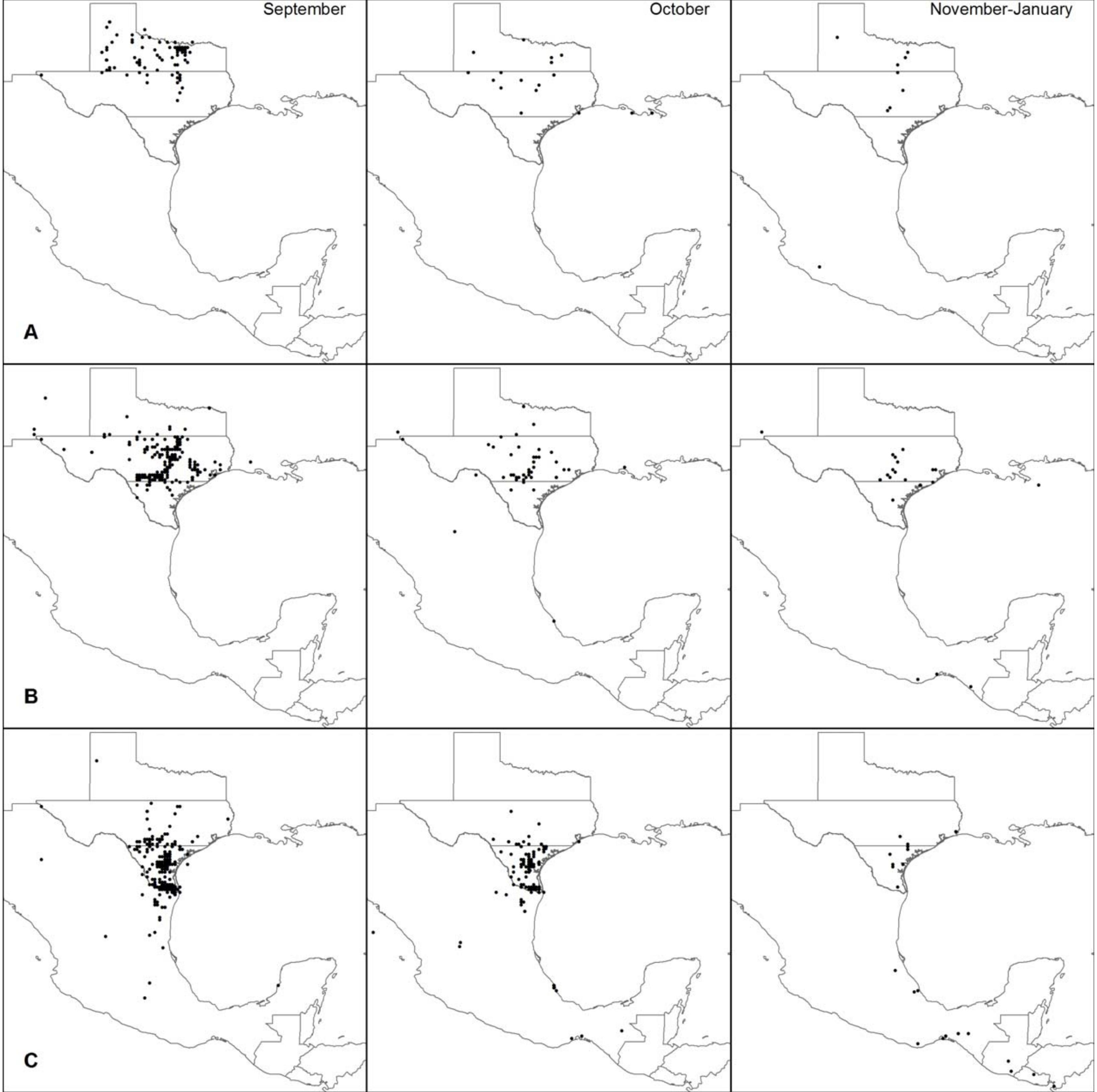
Banding Strata	Land area[a] weight	Mean breeding density	HY banded	AHY banded	Total banded[b]	w_J	w_A	w_T
A	26.15	0.87	4,640	2,362	7,002	0.49	0.96	0.32
B	33.91	2.11	10,802	9,057	19,859	0.66	0.79	0.36
C	8.56	3.07	20,715	12,489	33,204	0.12	0.21	0.08

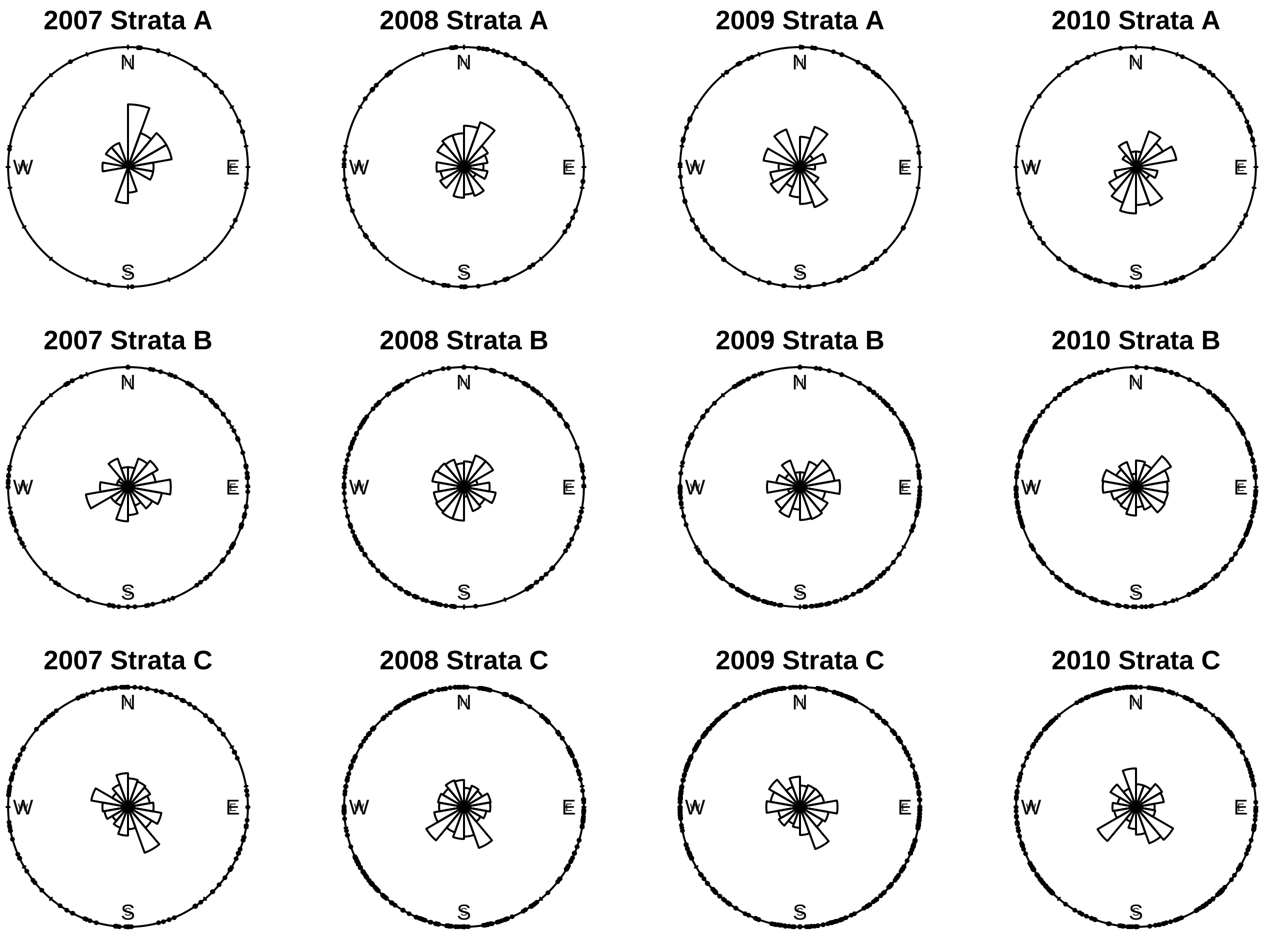
[a] Land weight area is calculated as the total area (km^2/100,000) of each strata.
[b] Note that the totals listed here are lower than totals in text due to removal of individuals with unknown age.

Table 5. Estimated age-specific and total derivation of harvest for white-winged doves banded in Texas based on direct recoveries from pre-season bandings conducted during 2007-2010.

			Age-specific recoveries		Age-specific contribution (%)		
Banding Strata	Recovery Strata	No. Recoveries	HY	AHY	HY	AHY	Total
A	A	128	101	26	11.75	12.59	12.07
	B	40	34	4	3.96	1.93	3.77
	C	1	1	0	0	0	0.09
B	A	19	14	3	2.19	1.19	2.01
	B	504	347	144	54.4	57.40	53.44
	C	30	23	6	3.61	2.39	3.18
C	A	2	2	0	0.05	0	0.05
	B	85	68	16	1.93	1.69	2.00
	C	992	775	215	22.09	22.78	23.38


A
B
C
32°0'0"N
29°0'0"N


September
October
November-January
A
B
C


2007 Strata A
2008 Strata A
2009 Strata A
2010 Strata A
2007 Strata B
2008 Strata B
2009 Strata B
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2007 Strata C
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2010 Strata C
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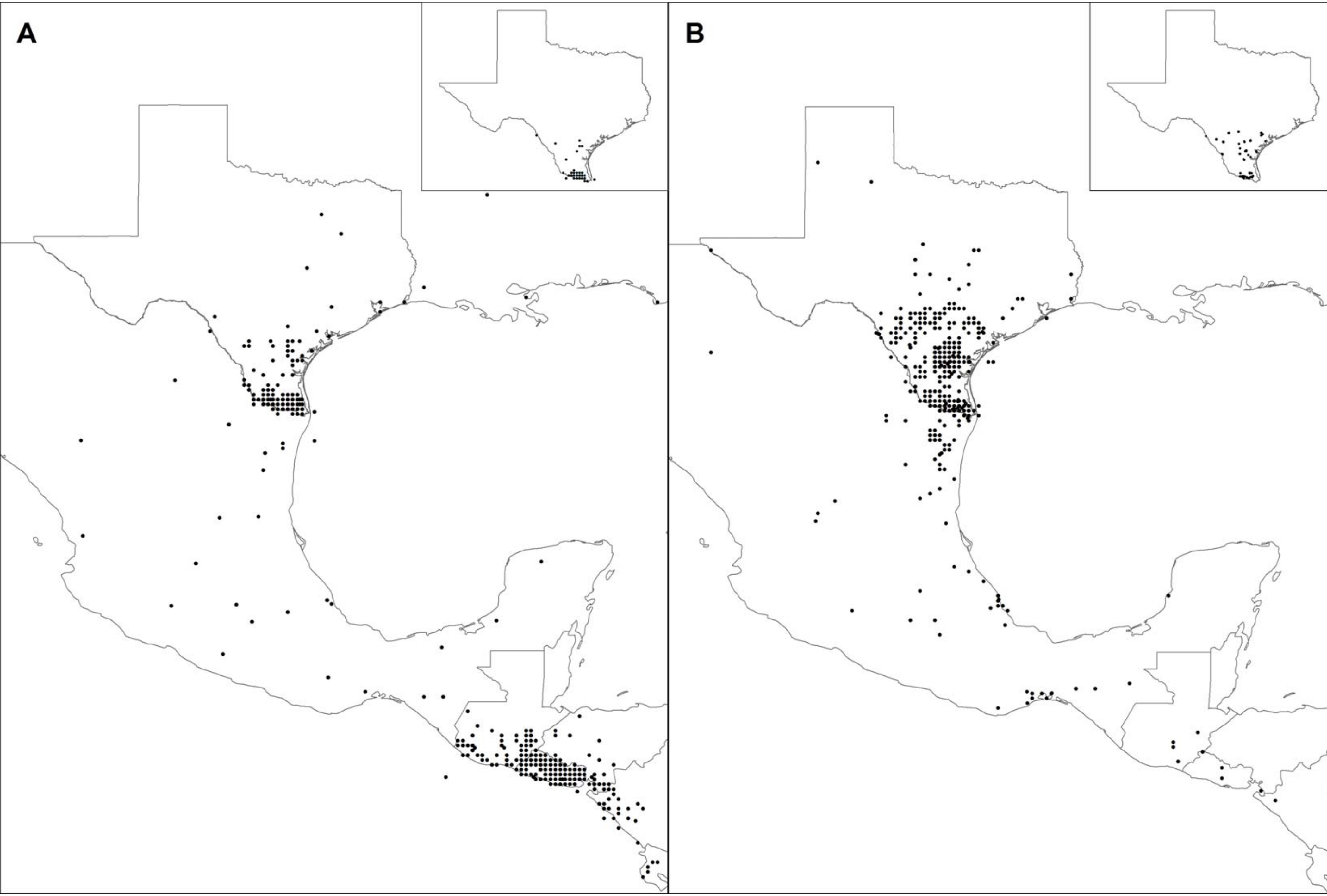
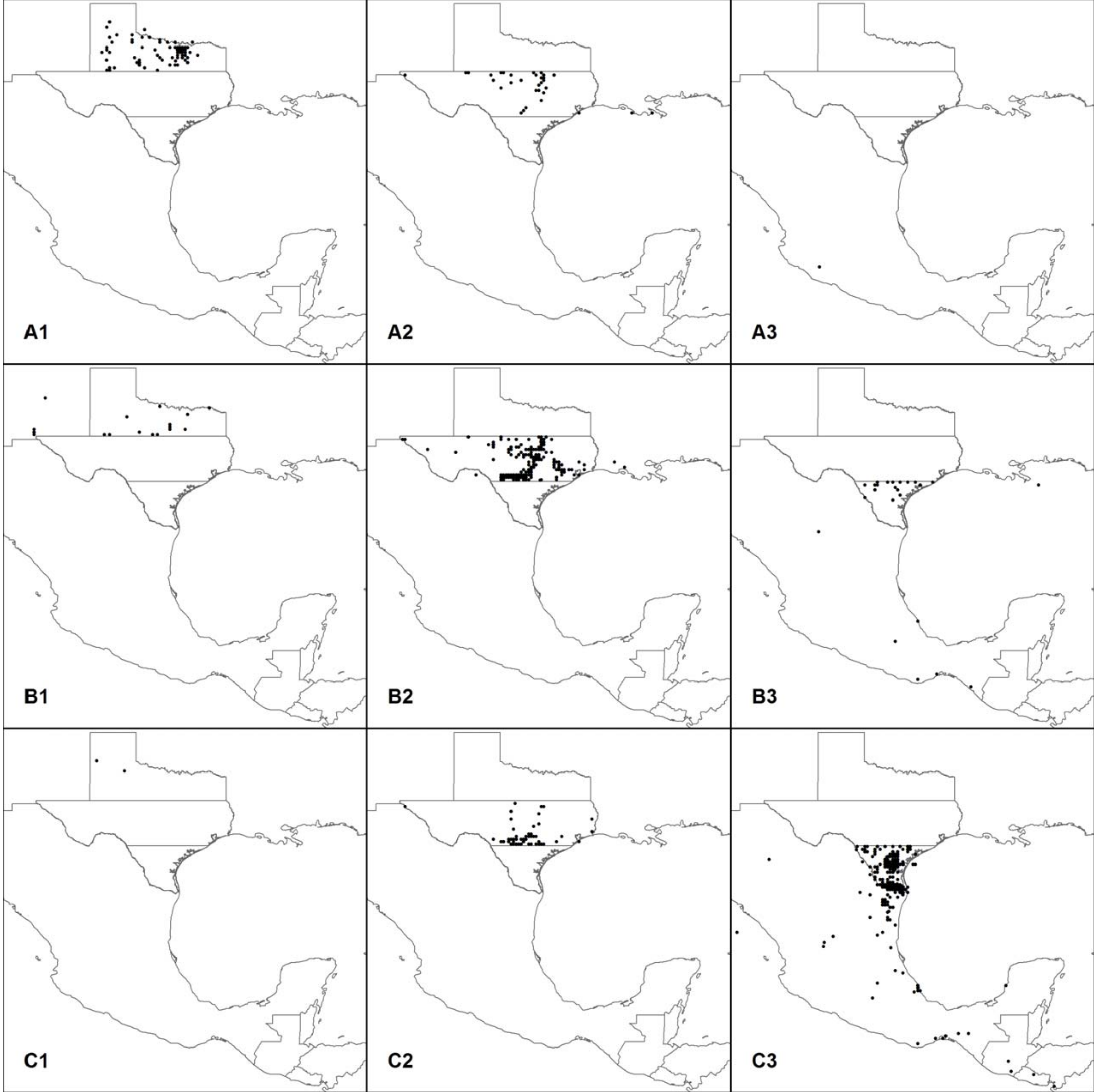

A
B



A1
A2
A3
B1
B2
B3
C1
C2
C3

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Survival, Fidelity, and Recovery Rates of White-winged Doves in Texas

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ABSTRACT Management of migratory birds at the national level has historically relied on regulatory boundaries for definition of harvest restrictions and estimation of demographic parameters. Most species of migratory game birds are not expanding their ranges, so migratory corridors are approximately fixed. White-winged doves (*Zenaida asiatica*), however, have undergone significant variation in population structure with marked range expansion occurring in Texas, and range contraction in Arizona, during the last 30 years. Because >85% of white-winged dove harvest in the United States (≈1.3 million annually) now occurs in Texas, information on vital rates of expanding white-winged dove populations is necessary for informed management. We used band recovery and mark-recapture data to investigate variation in survival and harvest across 3 geographic strata for white-winged doves banded pre-hunting

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season in Texas during 2007–2010. We banded 60,742 white-winged doves, recovered 2,458 bands via harvest reporting, and recaptured 455 known-age birds between 2007 and 2010. The best supporting model found some evidence for geographic differences in both hatch-year [juvenile; A = 0.205 (SE = 0.0476), B = 0.213 (0.0278), C = 0.364 (SE = 0.0254)] and after-hatch year [adult; A = 0.483 (0.0775), B = 0.465 (SE = 0.0366), C = 0.538 (SE = 0.251)] survival among strata. White-winged doves had a low probability of moving among strata (0.009) or being recaptured (0.002) across all strata. Harvest recovery rates were concordant with estimates for other dove species, but were variable across geographic strata. Based on our results, harvest management strategies for white-winged doves in Texas and elsewhere should consider differences in population vital rates among geographic strata.

KEYWORDS banding, harvest, multi-state capture recapture, site fidelity, survival, recovery rates, Texas, white-winged dove, *Zenaida asiatica*

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Informed harvest management of migratory birds calls for detailed knowledge of demographic parameters for use in mechanistic models to predict population response to environmental variation or alternative harvest scenarios (Williams and Johnson 1995, Runge et al. 2004, Otis 2006). Ideally, population models would synthesize existing data and provide insight into additional system parameters where further data acquisition should focus (Johnson and Kendall 1997). However, requisite data for model development is scarce for all but a few migratory game species (Nichols et al. 2007), thus hindering our ability to effectively manage species at the local, regional, and national scale. Doves (*Zenaida spp.*) represent one of the most widespread species in United States. Population estimates for doves exceed 300 million individuals (Otis et al. 2008), with an annual harvest of approximately 20 million, and >1 million hunters spending >3 million days afield annually pursuing doves (Raftovich et al. 2010). Due to tremendous interest in dove hunting and reported declines in mourning dove (*Z. macroura*) abundance (Sanders and Parker 2010), development of adaptive management strategies for mourning doves has garnered considerable management attention nationally in recent years (Otis 2002, Anonymous 2005, Otis 2006, Otis et al. 2008). As doves provide benefits to state and local economies, and often are the gateway for introducing individuals to hunting (Hayslette et al. 2001), both state and federal regulatory agencies have emphasized gathering information on mourning dove populations (Williams and Johnson 1995, Anonymous 2005, Otis 2009).

The white-winged dove (*Z. asiatica*) is less ubiquitous than the mourning dove, with a native range restricted to the southwestern United States and Mexico, and with introduced populations in Florida (Cottam and Trefthen 1968, George et al. 1994). Historically, white-winged doves were confined to semi-arid and arid habitats in the southwestern United States and Mexico (Schwertner et al. 2002); however, white-winged doves have slowly expanded their distribution by transitioning to urban environments across the southwestern United States (Rabe and Sanders 2010, Veech et al. 2011). In Texas, white-winged doves currently breed in >200 counties, excluding most of east Texas, whereas in 1980 only 10 counties in the Lower Rio Grande Valley had consistent white-winged dove breeding populations. Outside of the species' historic range in Texas, white-winged doves are confined almost exclusively to urban environments and preliminary evidence suggests most birds have developed breeding colonies in the residential centers of cities (Schwertner and Johnson 2005), with unknown impacts on population demography.

White-winged doves represent a significant recreational resource, with ≈1.3 million white-winged doves harvested annually in Texas, relative to a total annual harvest of ≈1.6

million harvested throughout the United States (Raftovich et al. 2010). Similar harvest levels likely occur in Mexico (Pacific Flyway Council 2003). Even though white-winged doves represent the second most harvested webless migratory game bird in the United States, and more white-winged doves are harvested annually in Texas than nationwide harvest for many waterfowl species (Raftovich et al. 2010), there has been little focus on collecting data requisite for supporting management planning for white-winged doves. The only current evaluation of population status for this species focused on Arizona (Rabe and Sanders 2010), with little discussion of white-winged dove status in California, New Mexico, and Texas (native ranges) or Florida (introduced range). Previous banding studies (George et al. 2000) advanced our knowledge on white-winged dove vital rates, but those data were collected between 1950 and 1980 in the Lower Rio Grande Valley and Mexico, thus it is unlikely that these data provide a representative evaluation of current population vital rates given the white-winged dove's range expansion in this region (Veech et al. 2011). For these reasons, lack of basic information on white-winged dove demography inhibits management, particularly because regulatory restrictions should be based on informed knowledge of a species' population dynamics (Williams and Johnson 1995, Otis 2002).

White-winged doves exhibit characteristics of a species that is both expanding its range within Texas and the Central Flyway, and potentially shifting from an annual migrant to resident, with unknown implications for population-level distribution, demography, and availability to harvest. Several studies have focused on demographic parameter estimation and provide insight into local population dynamics (Hayslette et al. 2000, Small et al. 2005). However, large scale banding studies are necessary to evaluate rangewide demography, potential implications of differential breeding stocks relative to harvest distribution and derivation (Collier et al. 2012a), and future impacts of regulatory actions and hunting activities (Otis and White 2002). As white-winged doves show high site fidelity and limited dispersal from natal environments to harvest location (Collier et al. 2012a), we expected that birds would remain faithful during the hunting season immediately post-banding to their original banding locations whether captured as hatch-year or after-hatch-year. During the course of our study Texas had 3 dove hunting zones separated by recognizable boundaries (e.g., interstate highways), so we created 3 strata similar to these zones (Figure 1). Strata A and B having the same regulatory structure (same season length, bag length, and opening day) while strata C opens approximately 20-25 days later and includes 2, 2 day special season hunting periods in the interim weekends between 1 September and opening of strata C during which mourning dove are limited to 4 per day in the bag.

Our objective was to evaluate variation in survival and harvest rates across geographic strata associated with the ongoing expansion of white-winged doves north through Texas relative to their historic breeding range in the Lower Rio Grande Valley (George et al. 1994, George et al. 2000) because regulatory programs that identify stock-specific management can be beneficial via reduced uncertainty regarding vital rates (Johnson and Moore 1996, Zimpfer and Conroy 2006). Additionally, we were interested in geographic fidelity and recovery of banded white-winged doves relative to capture stratum because a priori evidence (Collier et al. 2012a) has clearly shown regional fidelity of harvested birds, and thus may contribute to differential recovery rates. During our study, white-winged doves were banded using both toll-free and web-address bands, so we also used this opportunity to determine whether recovery rates differed by band designation type.

METHODS

Personnel from Texas Parks and Wildlife Department and Texas A&M University banded white-winged doves across Texas during March–August, 2007–2010. We captured and banded white-winged doves throughout this period using funnel-traps baited with standard bulk birdseed, black oil sunflowers and milo. All captured birds were aged (hatch-year: HY; after-hatch-year: AHY) based on gross morphological characteristics (Cottam and Trefthen 1968) and banded with United States Geological Survey Bird Banding Laboratory (BBL) size 4 aluminum bands. In 2007 we used only toll-free bands while in 2008–2010 we used used both toll-free and web-address bands in an approximate 50:50 split concurrent with the BBL shifting to a web-address return option; Sanders and Otis, In Press). Most (>95%) of our banding efforts were focused on white-winged doves in urban environments as dense white-winged dove breeding colonies have migrated to urban environments over the last 20 years (Schwertner and Johnson 2005).

We obtained banding and recovery data from the BBL in Laurel, Maryland. We included only normal, wild (BBL status code 3) white-winged doves banded in Texas by Texas A&M University, Texas Parks and Wildlife (TPWD) staff, and Texas Parks and Wildlife volunteers. Most (>96%) of doves were banded between 15 June and 15 August with the remainder banded between March and May during an intensive breeding population study during 2008 and 2009, which we do not expect to bias survival or recovery estimates. We did not include white-winged dove banding records from other banding projects because in many cases age codes were incomplete, we could not independently verify data accuracy, or toll-free and web-address bands were not used in an approximately 50:50 ratio during banding. We used records of inter-year recaptures of white-winged doves (e.g., doves banded in year t and recaptured during pre-hunting season banding in year $t+i$, $i = 1,\ldots, 4$) maintained by Texas Parks and Wildlife and Texas A&M

University, while recoveries of white-winged doves constituted those that were shot or found dead and reported during hunting season to the BBL. As the dove hunting season in Texas overlaps 2 calendar years, we designated each hunting season by the year in which it began (e.g., 2007 hunting season began 1 September 2007 and ended ~12 January 2008). We post-stratified banding and recovery data into geographic strata using the 10-minute latitude closest to each boundary on its western edge to designate strata (A = north banding stratum and recovery region, B = central banding stratum and recovery region, C = south banding stratum and recovery region) for our study (Figure 1).

We used a multi-strata mark-recapture and recovery model (Kendall et al. 2006) implemented in MSSRVRCV (Hines and Conn 2002) via R (R Development Core Team 2011). A R package (wwdoBR) containing all data and code is available from the primary author. We constructed multinomial models (White 1983, Hines and Conn 2002) to represent survival (S), strata-specific transition probabilities between sample (annual) periods (ψ), strata-specific transition probabilities between sample and recovery periods (τ), recapture probability (p), and recovery probability (f; Brownie et al. 1985). We modeled survival, recovery, and recapture parameters as age-, time-, and strata-specific, but constrained strata-specific transition probabilities (ψ) between sample periods to a constant for all models as our recapture data did not support detailed modeling of this parameter at an inter-strata or intra-annual basis (White 1983). We used an information-theoretic approach to model selection (Burnham and Anderson 2002) wherein we constructed a set of a priori candidate models for analysis (Table 1). We evaluated support for alternative models, given our data, using model rankings via Akaike's Information Criterion (AIC).

We considered 9 candidate models with survival and recovery probabilities varying by strata, age, band type, and time according to our initial hypotheses and descriptive evaluation of our band recovery data conducted previously (Collier et al. 2012a; Table 1). We constrained movement probabilities (ψ) across all models to be constant among strata as few doves (3%) were captured and then recaptured in a subsequent year within different stratum. Because of limited recaptures (<0.01% of total banded), we used either a constant or stratum- specific parameter for estimating recapture probability because time-dependent models led to over-parameterization. We fixed recovery transitions between banding stratum A and recovery region C and banding stratum C and recovery region A (Figure 1) to 0 ($\tau = 0$), as those transitions occurred only 3 total times during the course of our study. Because banding stratum B saw birds transition to both recovery region A and C in roughly equal proportions, we constrained τ to be equal for those strata transitions. Additionally, as we had no web-address bands during 2007, we fixed that parameter during analysis to 0.

RESULTS

We captured and banded 60,742 white-winged doves prior to the hunting season from 2007 through 2010 in Texas using 39,526 toll-free and 21,216 web-address bands. We banded 7,098 in the northern stratum (A), 20,300 in the central stratum (B), and 33,344 in the southern stratum (C; Figure 1). This included 23,908 AHY, 36,157 HY, and 677 unknown age-class birds. We recaptured 455 white-winged doves ≥1 year post initial banding. Ninety-seven percent (n = 441) of recaptured white-winged doves were recaptured within their original banding stratum. We recovered 2,458 white-winged doves via harvest between 2007 and 2010, comprised of 654 AHY, 1,776 HY, and 28 unknown age-class birds, with 1,583 toll-free and 875 web-address recoveries.

The best approximating model, S(age*strata), ψ(.), p(strata), f(age*strata*band), τ(strata), indicated that survival (S) rates were both age- and stratum-specific, transitions from banding to recovery strata were stratum specific, and recovery (*f*) rates varied by both age-, stratum-, and type-of-band-used-specific (Table 1). Models that did not address geographic structure in survival, recapture, or harvest had uniformly lower performance than models that included some geographic structure in these parameters. We based subsequent inferences on the best approximating model as all models incorporated the constraints detailed above to ensure numerical convergence, and as we found only limited model-based uncertainty (Table 1).

Predictably, stratum-specific HY survival of white-winged doves [A = 0.205 (SE = 0.0476), B = 0.213 (0.0278), C = 0.364 (SE = 0.0254)] was lower than AHY [A = 0.483 (0.0775), B = 0.465 (SE = 0.0366), C = 0.538 (SE = 0.251)], with the highest survival for both age classes occurring in stratum C (Figure 1). The probability of movement and recapture among strata was low [0.009 (SE = 0.025)], with recapture rates ≤2% across all strata [A = 0.017 (SE = 0.004), B = 0.021 (SE = 0.003), C = 0.016 (SE = 0.001)]. White-winged doves banded in stratum A were recovered in B [τ_{ij} = 0.19 (SE = 0.029)] more regularly than birds banded in stratum B were recovered in either A or C [τ_{ij} = 0.042 (SE = 0.007)], or birds banded in stratum C and recovered in B (τ_{ij} = 0.078 (SE =0.009)). The probability of white-winged doves being harvested within their original banding stratum was high (A = 0.81, B = 0.91, C = 0.92). Recovery probabilities ranged between 0.009 and 0.046 across age classes and recovery strata (Table 2), with HY recovery rates being approximately double AHY rates across all strata and showing an increasing trend from north to south. Finally, we found evidence for slight differences in recovery rates between toll-free and web-address band types, with web-address bands, with recovery probabilities being greater for web-address based in 5 of 6 stratum–class combinations and with recovery rates generally increasing from north to south (Table 2).

DISCUSSION

Annual survival probabilities for white-winged doves banded during our study exhibited both age- and stratum-specific variability, ranging from a low of 21% for HY white-winged doves in the northernmost stratum to a high of 54% for AHY birds in the southernmost stratum. Survival probabilities in stratum C for HY (36%) and AHY (54%) birds were lower than those of George et al. (2000) for HY (59%) and AHY (65%) white-winged doves banded in an area of south Texas equivalent to our stratum C during the 1960s. Not surprisingly, our results indicated that HY white-winged doves exhibited lower survival and greater harvest rates than AHY birds, which is consistent with George et al. (2000) and recent work on mourning doves (Otis et al. 2008). Similar to George et al. (2000), we found little evidence for annual variation in survival or recovery estimates. Recovery estimates from George et al. (2000) varied between 0.03 and 0.059 during their banding study, which were similar to our estimates for the same geographic stratum. Based on our results, variation in survival and harvest was attributable to geographic location rather than annual cycles, similar with recent estimates by Otis et al. (2008), who found stratum (state-level) estimates rather than year-specific estimates.

Although our model selection results indicated evidence of differences in band recovery rates by band type (i.e., toll-free and web-address), variation in recovery rates was low, typically with greater recovery rates for web-address bands than toll-free bands similar to results from Sanders and Otis (2011) and recovery rates increasing from north to south (Table 2). While variation in band reporting rates has implications for accurately estimating dove harvest and recruitment rates (Conroy and Blandin 1984, Otis et al. 2008), no rangewide operational banding of white-winged doves is currently ongoing; thus, any future banding operations for white-winged doves should use web-address bands eliminating the need for comparisons between reporting rates of different band types. Regardless, due to low band recovery rates across band types, we suggest that future efforts should focus on evaluating band reporting rates associated with reward banding (Tomlinson 1968, Nichols et al. 1991, Royle and Garrettson 2005, Otis et al. 2008).

Management of migratory birds at the national level has historically relied on designations of migratory corridors (e.g., flyways) that define regulatory boundaries for harvest and population monitoring (Munro and Kimball 1982, Sheaffer and Malecki 1996, Royle and Dubovsky 2001). However, knowledge of how vital rates vary spatially is important for regulatory planning (Munro and Kimball 1982, Johnson and Moore 1996) because the contribution of multiple breeding stocks to harvested populations can add additional complexity to models supporting harvest management decisions (Johnson and Moore 1996, Conroy et al. 2002). We found little evidence of white-winged dove movement between strata, with 97% of recaptured doves and 81-92% of recovered doves in the same stratum as when banded, contrary to the findings of Dunks et al. (1982) and Tomlinson et al. (1988) for mourning doves. We suggest that management for white-winged doves should consider spatially explicit substocks in Texas, and possible elsewhere within the nationally recognized dove harvest management areas (Keil 1959).

We investigated one a posteriori model wherein we combined the survival and recovery parameters for the north (A) and central (B) strata and re-evaluated our model predictions under the hypothesis that differences in vital rates in these 2 strata were not sufficiently different to warrant the increased regulatory complexity required by 3 Texas strata (Figure 1). Although this model was not originally posited as a potential candidate model, when integrated into our model selection results, the additional model was somewhat supported (ΔAIC = 3.7528) by our data. However, based on our a posteriori model, age-specific survival in the combined north-central banding strata [A+B; HY = 0.206 (SE = 0.024), AHY = 0.467 (SE = 0.034) and age-specific recovery rates for the same strata [HY = 0.031 (SE = 0.002), AHY = 0.015 (SE = 0.002)], are similar enough ($\leq$0.01 difference) to the stratum-specific estimates from our best approximating model that it may be worth considering strata A and B as a single management area in Texas. However, as survival is only one portion of those data necessary for harvest management planning, further information on variation in reproductive ecology, and the relationship between harvest and survival across geographic strata will be necessary for informed decision making before significant regulatory changes should be made.

White-winged dove populations in Texas have undergone continued expansion since the 1960s (Veech et al. 2011). Population vital rates mirror the white-winged dove expansion, with vital rates in the historic core of the species range (strata C; George et al. 1994) exhibiting higher levels of HY and AHY survival, and with survival decreasing for both age classes north of the historic range. As populations typically are more stable within their core ranges, and as demography is more stochastic at species range boundaries (Caughley et al. 1988, Lande 1991), it appears that white-winged dove vital rates are following expectations of an expanding population.

MANAGEMENT IMPLICATIONS

Our results provide demographic estimates for use in development of mechanistic population models that may in turn be used to inform harvest management decisions in Texas and possibly elsewhere. Assuming that white-winged dove populations exhibit vital rates that also are geographically specific, one implication of our research is that once identified, these geographic areas can be used to facilitate and inform banding programs for white-winged doves across the southwestern United States as outlined by Rabe and Sanders (2010). Additionally, until a national banding program for white-winged doves is implemented across the United States, our recovery rate estimates could be combined with age-specific harvest information collected via a parts collection survey to as recruitment monitoring to inform population management actions (Nichols and Tomlinson 1993). Finally, ongoing development of harvest management strategies for white-winged doves should focus on evaluating which geographic delineations are appropriate for harvest management planning as white-winged doves exist in a host of available habitats across the southwestern United States.

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Table 1. Model selection results for multi-strata (Figure 1) mark-recapture and recovery models for white-winged doves banded pre-hunting season in Texas 2007–2010, with parameters *S* (survival), ψ (movement), *p* (recapture probability), *f* (recovery rate) and τ (transition between banding and recovery strata). We provide Akaike's Information Criterion (AIC), AIC differences between models (ΔAIC), and model weights (w_i) relative to the -2 log-likelihood for the best fitting model (i.e., 1564.893).

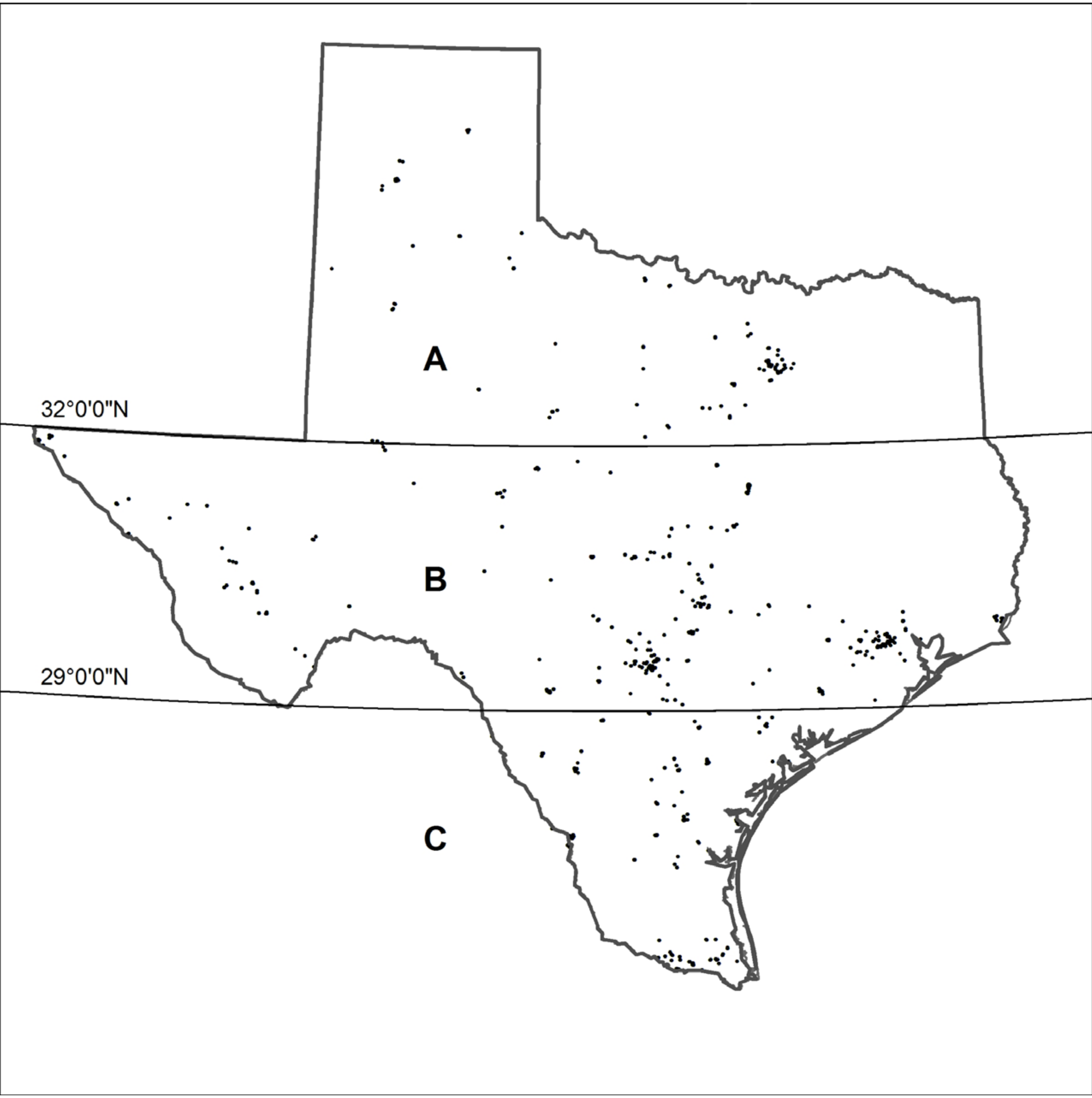
Model	No. of parameters	AIC	ΔAIC	w_i
S(age*strata), ψ(.), p(strata), f(age*strata*band), τ(strata)	25	1614.8933	0	0.9989
S(age*strata), ψ(.), p(strata), f(age*strata), τ(strata)	19	1629.8069	14.92	<0.0001
S(age*strata), ψ(.), p(strata), f(age*band), τ(strata)	17	1630.3026	15.41	<0.0001
S(age), ψ(.), p(.), f(age), τ(strata)	9	1677.8631	62.97	0
S(age), ψ(.), p(.), f(age*time), τ(.)	13	1741.8271	126.93	0
S(age*time), ψ(.), p(strata), f(age), τ(strata)	21	1818.0632	203.17	0
S(age*strata), ψ(.), p(strata), f(strata*band), τ(strata)	19	1819.2210	204.33	0
S(age*strata), ψ(.), p(strata), f(strata), τ(strata)	16	1834.6127	219.72	0

S(age*time), ψ(.), p(strata), f(strata), τ(strata)	18	1846.8892	231.99	0

Table 2. Estimated recovery probabilities for white-winged doves banded pre-hunting season in Texas, 2007–2010, categorized by harvest recovery stratum (Figure 1) based on best-approximating model.

		Band type	
Recovery Stratum	Age class[1]	Toll-free	Web-address
A	HY	0.0239 (0.0032)	0.0283 (0.00414)
	AHY	0.0107 (0.0022)	0.0093 (0.00252)
B	HY	0.0343 (0.0022)	0.0364 (0.00292)
	AHY	0.0163 (0.0014)	0.0197 (0.00198)
C	HY	0.0328 (0.0015)	0.0463 (0.00273)
	AHY	0.0183 (0.0011)	0.0206 (0.00167)

[1]Hatch-year = HY; After-hatch-year = AHY


A
32°0'0"N
B
29°0'0"N
C

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Immigration and Recruitment in an Urban White-winged Dove Breeding Colony

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ABSTRACT Dove population management necessitates estimates of vital rates for use in mechanistic models used to evaluate and predict population responses to environmental variation and/or alternative harvest scenarios. Estimating recruitment is complicated as a compendium of factors drive production in doves. White-winged doves (*Zenaida asiatica*) exhibit a fairly unique breeding strategy wherein they commonly return to the same breeding area and reproduce in

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large breeding aggregations (i.e., colonies). We used an open-population capture-recapture model to estimate immigration and in situ recruitment of white-winged doves breeding in an urban environment during 2009 and 2010. Immigration of adults into the breeding population peaked during late April and early May, with in situ recruitment occurring during a 6-week period from 19 June to 30 July. Our results predicted that >90% of all hatch year individuals had entered the local population by 1 August. Based on our results, we suggest a new protocol for recruitment monitoring wherein managers could conduct 2 breeding population surveys, mid-May to estimate adult population size and late July or early August to estimate combined juvenile and adult population size and use the ratio (N_{t+1}/N_t) to estimate annual recruitment. The Jolly-Seber approach we applied allows white-winged dove production to be estimated directly while separating immigration from in situ recruitment and as such is useful for predicting per capita annual recruitment for use in harvest management planning.

KEYWORDS capture-recapture, immigration, Jolly-Seber, POPAN, population growth, white-winged dove, *Zenaida asiatica*

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Doves (*Zenaida spp.*) represent some of the most widespread species in United States, with population estimates exceeding 300 million individuals and harvest exceeding 20 million birds annually (Otis et al. 2008, Raftovich et al. 2010). As doves grant substantive benefits to state and local economies, and often provide a gateway for introducing individuals to hunting (Hayslette et al. 2000), both state and federal regulatory agencies have emphasized garnering information on dove populations (Williams and Johnson 1995, Anonymous 2005). Moreover, dove-population management necessitates estimates of vital rates for use in mechanistic models used to evaluate and predict population responses to environmental variation and/or alternative harvest scenarios (Williams and Johnson 1995, Runge et al. 2004, Otis 2006). Ideally, vital rate data across age and sex would be available for modeling population trajectories (Johnson and Kendall 1997); however, this is rarely the case for doves or most other migratory birds (Nichols et al. 2007).

Annual reproduction is one of the most critical components underlying dove population trajectory; however, the process of annual recruitment by doves is poorly understood due to long breeding seasons, non-standardized sampling methods used across the range of these species, and the typically short timeframes of most monitoring programs (Geissler et al. 1987, Otis 2003). Estimating production (and hence recruitment) is additionally complicated as a compendium of factors (i.e., nesting chronology, laying rate, egg hatchability, nest survival, fledgling survival) drive production in doves (Geissler et al. 1987, Sayre and Silvy 1993) necessitating that models be used to predict recruitment (Otis 2003). For most harvested migratory species, the U.S. Fish and Wildlife Service (USFWS) relies on a parts collection survey (PCS) to index reproduction (Miller and Otis 2010). Age ratio data, or the number of juveniles to adults estimated from harvested birds, are used to index reproduction and drive harvest management planning at the national scale (Nichols and Tomlinson 1993, Zimmerman et al. 2010). Alternatively, several reverse-time capture-recapture approaches are available that estimate annual recruitment directly (Pradel 1996, Nichols et al. 2000, Link and Barker 2005). Reverse-time approaches, however, assume an inter-annual cycle of data collection and estimates of recruitment represent both those individuals transitioning between juvenile and adult age classes as well as individuals entering via immigration (Pradel 1996, Nichols et al. 2000). Thus, recruitment is defined as the number of new individuals relative to the number of old individuals, rather than the familiar biological definition that relates recruitment to in situ production and that PCSs attempt to measure (Nichols and Pollock 1990).

The white-winged dove (*Z. asiatica*) is less ubiquitous than the mourning dove (*Z. macroura*), with a native range restricted to the southwestern United States and Mexico, and an introduced population in Florida (Cottam and Trefethen 1968, George et al. 1994). White-winged doves exhibit a fairly unique breeding strategy wherein they commonly return to the same breeding area annually and reproduce in breeding aggregations (i.e., colonies) sometimes exceeding 1,000 nests/ha (Cottam and Trefethen 1968, Nichols et al. 1986, George et al. 1994). Historically, Texas breeding colonies of white-winged doves occurred in native brushland and citrus orchards in the Lower Rio Grande Valley (Marsh and Saunders 1942, Cottam and Trefethen 1968, Martinez et al. 2005). Although it has been suggested that white-winged doves in this region suffered from poor reproduction since at least 1969 (Hayslette et al. 1996), this species rapidly expanded its range northward and established new breeding colonies in urban environments across Texas and the southwestern United States during the last few decades (George et al. 1994, Schwertner and Johnson 2005, Veech et al. 2011).

In an effort to further our understanding of white-winged dove annual reproduction as a basis for future conservation planning, we evaluated in situ recruitment of white-winged doves in an urban breeding colony in Texas. We applied an open population capture–recapture approach to identify peak arrival and breeding periods, estimate age-specific entrance via immigration and *in situ* recruitment over the course of the breeding season, and estimated age-specific abundance and recruitment (juvenile to adult ratio; Otis 2003) for white-winged doves during 2009 and 2010.

METHODS

We banded white-winged doves in Alice, Texas (Latitude 27.25, Longitude -98.07) during February–August, 2009–2010. We captured white-winged doves using funnel-traps baited with standard bulk birdseed, black oil sunflower, and/or milo. All captured birds were aged (hatch-year: HY; after-hatch-year: AHY) based on gross morphological characteristics (Cottam and Trefethen 1968) and banded with U.S. Geological Survey (USGS) size 4 metal bands (2007: used toll-free bands; 2008–2010: used both toll-free and web-address bands in an approximate 50:50 split concurrent with the USGS shifting to a web-address return option; Sanders and Otis 2012, Collier et al. 2012b).

We used an open population capture–recapture approach (i.e., Jolly-Seber; Schwarz et al. 1993, Schwarz and Arnason 1996) to model survival, recruitment, and to estimate period-specific population size for HY and AHY white-winged doves in our urban breeding colony during 2009 and 2010. We categorized the reproductive season into 13, 2-week periods beginning 27 February and ending 31 August and aggregated multiple recaptures within a 2-week period as a single capture for analysis. We used MARK (White and Burnham 1999) via RMark (Laake and Rexstad 2009) to implement a POPAN model (Schwarz and Arnason 1996) for analysis (see supplement).

Our approach hypothesized a super-population (N) for which occasion-specific (N_i) estimates of abundance and entry (b_i) were based (Schwarz and Arnason 1996). Thus, use of individual covariates or other constraints were difficult to implement and as such our candidate models relied on modeling age-specific and temporal variation in immigration and birth rates as these parameters were the primary focus of our study. Our approach is similar to escapement modeling detailed by Schwarz et al. (1993), wherein we were able to separate within year immigration of AHY individuals from HY individuals fledged in the colony. Because trapping was initiated well before immigration occurred, entry (b) parameters for AHY individuals represented recruitment of new adults into the breeding colony over the course of the breeding season (immigration). Based on our capture data, HY individuals did not begin to appear until early June of each year, so we fixed both the survival (Φ) and entry (b) parameters at 0 for the first 6 sampling occasions (27 Feb–21 May). The formulation for the super-population approach estimated the number of individuals that had immigrated (arrived) before sampling began as a derived parameter with probability (b_0) equal to 1 minus the sum of the entrance probabilities for all sampling occasions. In our situation, however, there were no individuals in our study area before trapping was initiated (Schwarz et al. 1993). Thus, we created an artificial sampling occasion for period $t-1$ in our data matrix during which there were no captures for either age class such that estimates of b_0 were then conditioned on that sampling occasion. This forced the estimated probability associated with b_0 to be negligible and ensured that entry parameters (b_i) in our model summed to 1 for both HY and AHY classes (see supplement).

We attempted to use the same modeling approach for both years of data; however, during 2010, capture of HY individuals was significantly lower (~80%) than during 2009. Subsequently, the number of recaptures available was negligible for 2010, precluding accurate parameter estimation using biologically sensible capture-recapture models of in situ HY recruitment and abundance. Thus, for 2009, we provided estimates of apparent survival, immigration, and abundance for AHY individuals, and *in situ* reproduction of HY individuals, but for 2010, we report apparent survival, immigration, and abundance for adults.

RESULTS

We captured 5,101 unique white-winged doves in 2009 (2,894 AHY, 2,207 HY) and 3,502 unique white-winged doves in 2010 (3,106 AHY, 486 HY). Using our 2009 data, we were able to fit a full group (age class) by time model for both apparent survival and recapture probability (Table 1). For the 2010 data, models with a full group by time effect, as well as a time only effect in recapture were considered plausible. Because so few HY birds were recaptured post initial marking (<10) during 2010, the full group by time model rendered several parameters inestimable (Schwarz et al. 1993); thus, we did not model average and based our 2010 estimates of adult entry and abundance on a model that constrained recapture rates to be time, but not group specific (Table 1).

As trapping was initiated before we assumed doves had arrived, the small number of individuals from the total breeding population the model predicted would be present before sampling began in 2009 (0.003%) and 2010 (0.01%) indicated that few, if any doves were present before sampling began, thus reducing potential biases in the underlying recruitment distribution (Schwarz et al. 1993). Immigration of AHY white-winged doves consisted of 2 distinct pulses (Table 2). The first pulse initiated in early March, peaked around mid-April, and declined through early June. The second pulse initiated during late June, peaked in mid to late July, and declined to the point where no new birds entered the population by late August (Table 2). During both years, there was a distinct period from 22 May to 4 June where entry probabilities for both AHY and HY were minimized, which occurred roughly 2–4 weeks before the HY individuals entered the population en masse (Table 2). In situ recruitment occurred during a 6-week period from 19 June to 30 July, where our models predicted that >90% of all HY individuals entered the local population before 1 August (Table 2). Occasion-specific apparent survival was fairly consistent across sampling periods; however, in 2010 we had several inestimable parameters during the course of modeling due to sparse recapture data during those capture periods (Table 3).

DISCUSSION

The Jolly-Seber approach we applied allows white-winged dove production to be estimated directly while separating immigration from in situ recruitment (Nichols and Pollock 1990, Schwarz and Aranson 1996). Based on our estimates for HY and AHY population size in 2009, per capita recruitment (N_{HY}/N_{AHY}) was 1.31 HY individuals per AHY bird. Assuming a 50:50 sex ratio, our data equate to a production estimate of 2.6 HY birds per AHY pair; this falls within the range predicted by Otis (2003) for mourning doves within the south-central United States. Recruitment estimation is complicated as it is inherently a function of several parameters (e.g., nesting rate, nest survival, fledgling survival) and rarely are resources available to measure all metrics on any single population over time. Thus, methods resulting in predictions of per capita annual recruitment (N_{HY}/N_{AHY}; Nichols and Tomlinson 1993) into the harvestable population are useful for management. Several authors have conducted research addressing breeding season ecology on white-winged doves (Alamia 1970, Swanson and Rappole 1993, Schacht et al. 1995, Hayslette et al. 1996, Hayslette and Hayslette 1999, Small et al. 2005); to our knowledge, we were the first to estimate actual production in white-winged doves, rather than relying on egg/fledgling density, nest success, or other parameters as proxies for recruitment.

During both years of our study, AHY captures were near 0 during the period 22 May–4 June. Reduced captures within this period occurred several weeks before 50% of the HY individuals in 2009 were predicted to enter the population. As white-winged doves have a 15–20 day incubation followed by 13–18 days in the nest before fledging (Schwertner et al. 2002), this places the peak production of HY individuals entering the population around 27 May, or roughly in the middle of the 22 May–4 June period. Thus, the low capture rate of AHY during this time was likely due to adults tending to incubation or nestlings. We note that our results also indicate a pulse of AHY individuals entering the local breeding population during the identified peak of HY entry during both years (Table 2). Based on available knowledge of white-winged breeding biology, we expect that these individuals likely failed initial nesting attempts and were emigrating into other breeding populations before fall migration began (Alamia 1970, Schwertner et al. 2002).

During 2010, HY captures were limited to primarily 1 capture for each individual, whereas AHY captures remained similar to 2009 levels. No changes were made to our study location, trapping locations, trapping effort, or study timing between years. Our 2009 study period occurred during the final year of a significant drought in Texas, whereas normal precipitation occurred during the spring and summer of 2010. We suggest 2 plausible explanations for why HY captures were so low during 2010: 1) production during 2010 actually was subnormal and subsequently there were lower numbers of HY individuals available within our study area for capture, or 2) mast-based food sources were readily available to HY individuals post fledging, which reduced trapping efficiency at our study site.

Although our intensive capture–recapture data were necessary for initial evaluation of immigration and breeding season timing of white-winged doves, our results provide a foundation for us to suggest potential alternative monitoring protocols for white-winged dove recruitment in Texas. Previous work on timing of breeding activity indexed via coo counts (Sepulveda et al. 2006) indicated that peaks of calling occurred in early May, which from our data would be roughly concordant with our estimates of reproductive timing. Managers could conduct visual breeding population surveys during mid-May to estimate AHY population size, and then repeat the survey in late July or early August to estimate abundance when a majority of HY birds has entered the local population but before migration occurs. Then, straightforward application of a simple population growth estimator ($\lambda = N_{t+1}/N_t$) could be used to estimate *in situ* recruitment. Because white-winged doves have transitioned to urban environments (Schwertner and Johnson 2005, Collier et al. 2012a, Collier et al. 2012b), our information on the timing of adult immigration and in situ recruitment could make the estimation of recruitment via count statistics a plausible option for supporting future conservation and harvest management planning strategies. Such density and recruitment information could be used for initial comparison to future PCS data collected by the USFWS for monitoring local populations, which could be used to support better management of white-winged doves.

Alternative recruitment estimation methods (Pradel 1996, Nichols et al. 2000, Link and Barker 2005) tend to define recruitment as a function of the number of new individuals relative to the number of old individuals in the population of interest. However, the length of the sampling interval must allow for maturation such that individuals transition from juvenile to adult between sampling occasions. These approaches work well for individuals trapped on an annual basis, but do not represent population-level juvenile recruitment. However, our approach using a Jolly-Seber model has rarely been applied to situations where estimates of both immigration and in situ production are needed for management planning. Solutions focused on estimating in situ recruitment can benefit from the Jolly-Seber design used here, or one of the various closed or open robust design applications (Nichols and Pollock 1990, Kendall and Bjorkland 2001).

MANAGEMENT IMPLICATIONS

Our study provides the first direct estimates of white-winged dove breeding colony immigration and in situ recruitment into an urban breeding colony in Texas. While limited in scope and scale, our estimates of HY per AHY were concordant with previous estimates of dove recruitment within the range of our study area that used a composite set of parameters as proxies for recruitment. Our results are directly useful for future white-winged dove conservation and management and provide a foundation for further investigation into population dynamics of urban doves. Moreover, data on the timing of immigration and recruitment supports the potential for use of independent approaches for monitoring recruitment and thus enabling flexibility in development of long-term management strategies.

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Table 1. Model selection table for models fitted to 2009 and 2010 white-winged dove capture-recapture data in Alice, Texas, USA.

2009	*k*	AIC_c	ΔAIC_c	w_i
Φ(g*t), p(g*t), pent(t), N(g)	58	17,552,17	0	0.99993
Φ(g*t), p(.), pent(t), N(g)	36	17,571.07	18.89	0.00007
Φ(g*t), p(t), pent(t), N(g)	49	17,575.44	23.26	0
Φ(t), p(.), pent(t), N(g)	29	17,587.62	35.45	0
Φ(Age), p(.), pent(t), N(g)	18	18,334.37	782.19	0
Φ(.), p(.), pent(t), N(g)	17	18,646.13	>1093	0
2010				
Φ(g*t), p(t), pent(t), N(g)	49	18,915.38	0	0.8259
Φ(g*t), p(t*g), pent(t), N(g)	58	18,918.49	3.11	0.1740
Φ(g*t), p(.), pent(t), N(g)	36	18,953.76	38.38	0
Φ(t), p(.), pent(t), N(g)	29	18,994.22	78.85	0
Φ(Age), p(.), pent(t), N(g)	18	19,241.80	326.42	0
Φ(.), p(.), pent(t), N(g)	17	19,321.25	>405	0

Table 2. Sampling occasion specific estimates of entry via immigration (b_{AHY} (SE)), entry via in situ recruitment (b_{HY} (SE)), and age-specific abundance (95% CI) for white-winged doves banded in Alice, Texas, during 2009 and 2010.

	2009				2010[a]	
Occasion	b_{AHY}	N_{AHY}	b_{HY}	N_{HY}	b_{AHY}	N_{AHY}
1	0.003 (0.001)	29	0	0	0.01 (0.001)	153
2	0.05 (0.025)	456	0	0	0.14 (0.05)	2065
3	0.03 (0.023)	289	0	0	0.07 (0.029)	1041
4	0.54 (0.12)	4742	0	0	0.157 (0.042)	2244
5	0.16 (0.095)	1390	0	0	0.138 (0.039)	1976
6	0.074 (0.026)	652	0	0	0.152 (0.041)	2169
7	0[b](0)	3	0.002 (0.0009)	27	0[b](0)	57
8	0.003 (0.001)	27	0.023 (0.012)	267	0.018 (0.005)	262
9	0.067 (0.017)	587	0.502 (0.185)	5746	0.062 (0.031)	882
10	0.035 (0.012)	306	0.262 (0.122)	2998	0.131 (0.063)	1858
11	0.020 (0.008)	182	0.156 (0.077)	1782	0.105 (0.078)	1497

12	0.003 (0.0003)	32	0.027 (0.011)	313	0[b](0)	0
13	0.001 (0.005)	13	0.011 (0.039)	130	0[b](0)	0
Abundance		8,714		11,431		14,221
		(6,835–11,489)		(6,263–23,184)		(11,398–17,993)

[a] Due to limited recaptures we were unable to estimate *in situ* recruitment during 2010

[b] Inestimable parameter due to limited recaptures during that occasion

Table 3. Sampling occasion specific estimates of apparent survival for hatch year (Φ_{HY}) and after hatch year (Φ_{AHY}) individuals for 2009 and 2010 based on white-winged doves banded in Alice, Texas, during 2009 and 2010. Inestimable parameters are denoted (ne) and represent those parameters that were either confounded (Schwarz et al. 1993) or for periods where recapture data were too sparse for estimation (e.g., survival when no individuals were present) are represented as a zero.

	2009		2010
Occasion	Φ_{AHY}	Φ_{HY}	Φ_{AHY}
1	0	0	0
2	ne	0	0.76 (0.21)
3	0.51 (0.002)	0	0.30 (0.07)
4	0.53 (0.14)	0	0.48 (0.08)
5	0.34 (0.04)	0	0.34 (0.05)
6	0.45 (0.03)	0	ne
7	ne	0	0.85 (0.14)
8	0.68 (0.08)	0.29 (0.16)	0.60 (0.20)
9	0.42 (0.08)	0.52 (0.16)	ne
10	0.45 (0.10)	0.60 (0.16)	0.42 (0.24)
11	0.54 (0.18)	0.21 (0.06)	ne
12	0.08 (0.03)	0.05 (0.009)	ne
13	ne	ne	ne