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ABSTRACT—We examined key factors thought to influence Mourning Dove (*Zenaida macroura*) nest density (nests/ha) in Blue Oak woodlands (*Quercus douglasii*), riparian woodlands (*Salix* spp., *Populus fremontii*), and commercial walnut (*Juglans* spp.) orchards in northern California (north of UTM: Zone 51N, 324397E, 4207703N, datum WGS84). We hypothesized that nest density could be used to characterize the suitability of habitats for breeding Mourning Doves because nest success has often been shown to not vary predictably by habitat type. Because weather does affect nest success, we examined the influence of spring rainfall and ambient temperature, as well as habitat on nest density. We recorded all Mourning Dove nests found in surveys conducted every 3rd wk from mid-April to mid-August, which encompassed the nesting season, in each of 6 to 10 randomly placed survey plots in each of 4 study areas during 1992–1995, with a supplemental survey during September 1994. Survey date, habitat type, and spring weather affected period nest density (PND; mean number of all active nests/ha present during any given survey); and habitat type and weather affected cumulative nest density (CND; total number of different nests produced annually/ha). Seasonally, PND was relatively low in April, high from May to July, lower in August, and zero by September. Riparian woodlands tended to support higher PND and CND compared to walnut orchards and Blue Oak woodlands in that order. This effect was pronounced during the warm-dry springs of 1992 and 1994, but was not always evident during the relatively cool-wet springs of 1993 and 1995 (weather characterized relative to April mean high temperature and March to May mean rainfall). The best predictive model (lowest AIC_C) for PND contained a quadratic trend with survey timing, and effects due to habitat type, high temperature and rainfall deviations from long-term average, number of rain-days, and tree density. The best model for CND contained habitat, temperature, rainfall, rain-days, and tree density. Nest success increased at a declining rate as nest density increased in Blue Oak and riparian woodlands, demonstrating probable density-dependent resource or mortality limits on nest success that did not affect nest density within the ranges we recorded. Nest density measures should be useful to land managers in assessing responses of nesting Mourning Doves to available nesting habitats and local spring weather.

Key words: Blue Oak woodlands, California, Mourning Dove, nest density, nest success, orchards, riparian woodlands, season, weather, *Zenaida macroura*

Miller and others (2001a) studied nest success (% of nests that fledge young) of Mourning Doves (*Zenaida macroura*) in orchards and native habitats in northern California in response to a long-term decline in western breeding populations (Dolton and others 2008). They found that nest success did not predictably vary by habitat type, a typical result for Mourning Doves

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(Randall 1955; Caldwell 1964; Best and Stauffer 1980; Westmoreland and Best 1985; Olson and others 1991; Drobney and others 1998; Hayslette and others 2000; Stoleson and Finch 2001). Because nest success is the demographic variable most often used to characterize avian habitat quality or fitness potential (Coon and others 1981; Johnson 2007), nest success would be problematical as a method to index habitat quality of Mourning Doves. Western Mourning Dove populations have not increased (Dolton and others 2008) since the work of Miller and others (2001a), even though these investigators found that production of young per pair relative to mortality was sufficient to enable populations to grow (Tomlinson and others 1988). Therefore, factors other than nest success and survival demographics must be involved in habitat productivity for Mourning Doves.

We propose that nest densities of Mourning Doves should be associated with the fundamental or inherent quality of specific habitat types (Johnson 2007). Habitat-specific limits on nest density could constrain Mourning Dove populations if region-wide declines of various habitat types include those with the highest Mourning Dove nest densities, as proposed by Miller and others (2001b). There is abundant evidence that Mourning Dove nesting density often varies by habitat type (Hopkins and Odum 1953; Wolfenden and Rohwer 1969; Olson and others 1991; Drobney and others 1998; Hayslette and others 2000; but see Stamp 1978), and it follows that nest density could be used to characterize Mourning Dove nesting habitat quality, ideally together with nest success and adult survival (Johnson 2007). There is still uncertainty, however, about this because there is a strong spring weather component in Mourning Dove nest success that could also affect nest density (Hanson and Kossack 1963; La Perriere and Haugen 1972; Morrow and Silvy 1982; Miller and others 2001a).

Blue Oak (*Quercus douglasii*) woodlands, mixed willow (*Salix* spp.) and Fremont Cottonwood (*Populus fremontii*) riparian woodlands, and some commercial orchards provide crucial nesting substrates for Mourning Doves in California (Miller and others 2001a). Blue Oak woodlands cover vast areas of the foothills of the Sierra Nevada and Coast Range Mountains surrounding the northern Central Valley (Bolsinger 1988; Gaman and Firman 2006); riparian woodlands, though greatly reduced (Katibah 1984), grow quickly (Anderson and Ohmart 1984) and still occur with Central Valley rivers, streams, canals, stock ponds, marshes, and lakes (Smith 1977); and commercial orchards, which can be important Mourning Dove nesting habitat (Knight and others 1984; Miller and others 2001a), have expanded markedly in the northern Central Valley in recent decades (National Agricultural Statistics Service 2009). These 3 habitat types are included in annual Mourning Dove call-count routes in California that index population trends (Dolton 1993). Therefore, we chose these habitat types in which to study Mourning Dove nesting density concurrently with nesting success studies in the same habitats (Miller and others 2001a).

We had 2 principal objectives for our research: (1) Examine how seasonal chronology of the nesting season, habitat type, weather (temperature, precipitation), and tree density influence nesting density of Mourning Doves in Blue Oak woodlands, riparian woodlands, and walnut (*Juglans* spp.) orchards; and (2) examine the relationship between Mourning Dove nest density and nest success in these habitats. These data should contribute to basic understanding of factors that influence the way that Mourning Doves distribute themselves in various important nesting habitats.

Methods

Study Areas

We studied Mourning Dove nesting density at 4 tree-dominated areas in northern California during March through August 1992 to 1995 (through September in 1994). These areas included Gray Lodge Wildlife Area (396578E, 4354455N) and private lands east of Lodi (332020E, 4222345N) during 1992 to 1995; Spenceville Wildlife Area (348709E, 4331181N) during 1993 to 1995; and Gray Davis Dye Creek Preserve (419026E, 4439289N) during 1994 and 1995 (all UTM locations are zone 51N, datum WGS84). Miller and others (2001a) studied Mourning Dove nest success concurrently on these same areas. A full description of each study area, including locations, vegetation type, extent of each vegetation type in California, and general land management, is available in Miller

and others (2001a). The Mourning Dove nesting habitats consisted of Blue Oak woodlands at Spenceville and Dye Creek, mixed willow and Cottonwood riparian woodlands at Gray Lodge, and privately owned commercial walnut orchards near Lodi. Although our study lacks landscape scale replication beyond these 4 sites, we assumed that the patterns in nesting density across these sites were likely driven by habitat type.

We annually characterized weather at our study areas using temperature and rainfall data from weather stations <20 km from each area (Miller and others 2001a). We used deviations from average high temperature in April and deviations from average rainfall, as well as total number of days with rain (rain-days), from March through May (spring). Because we did not include all 4 study areas each year, we used average weather data from 1971–2000 (National Oceanic and Atmospheric Administration 2002) for Gray Lodge and Lodi (2-area average) during spring 1992, the 2 areas we worked that year. Likewise, we averaged weather data for Gray Lodge, Lodi, and Spenceville during 1993 (3-area average); and we averaged data for all 4 study areas during 1994 and 1995 (4-area average). We did not use summer weather to characterize our study areas because a hot, dry weather pattern routinely prevails after May and continues through September, coincident with the normal cessation of seasonal rainfall (Major 1995).

Spring weather conditions differed by year in the study region (National Oceanic and Atmospheric Administration 1992–1995). Relatively warm and dry (warm-dry) conditions prevailed during spring 1992 and 1994: (1) average high temperature in April exceeded by 2.4°C (s_x = 0.4) the 2-area average of 22.8°C in 1992, and the 4-area average of 22.8°C by 1.1°C (s_x = 0.4) in 1994; (2) average spring rainfall was 2.14 cm (s_x = 0.25) below the 2-area average of 11.29 cm in 1992, and 5.94 cm (s_x = 1.57) below the 4-area average of 13.18 cm in 1994; and (3) rain-days averaged 13 d each in 1992 (s_x = 0.0) and 1994 (s_x = 3.0). In contrast, relatively cool and wet (cool-wet) conditions occurred during 1993 and 1995: (1) average high temperature in April fell 0.6°C (s_x = 0.3) below the 3-area average of 23.0°C in 1993, and 1.4°C (s_x = 0.5) below the 4-area average of 22.8°C in 1995; (2) average spring rainfall was 1.17 cm (s_x = 1.57) above the 3-area average of 12.38 cm in 1993, and 17.21 cm (s_x = 2.28) above the 4-area average of 13.18 cm in 1995; and (3) rain-days averaged 19 d (s_x = 2.0) in 1993 and 28 d (s_x = 3.0) in 1995.

Survey Plots

All density surveys were located within the same study areas used for the concurrent Mourning Dove nesting success study (Miller and others 2001a). We used 10 randomly located rectangular plots to study Mourning Dove nesting density at Gray Lodge and Lodi. We located the plots at Gray Lodge in riparian vegetation along irrigation canals and dirt or grass-covered roads or trails. Each plot was 200 m long and 15 to 24 m wide, reflecting variable widths of riparian zones, and totaled 3.5 ha. The plots contained an average of 214 (s_x = 46) trees/ha (tree density), consisting of 69% mixed willow and 31% Cottonwood. Sampled areas included a mix of riparian corridors, including those passing through open grasslands or wetlands (dry for most of field seasons), those within areas of widely scattered trees, and those within areas of semi-open woodlots of mature trees with understory. At Lodi, we randomly placed the 10 rectangular plots, which had somewhat varying dimensions reflecting different tree sizes and spacing, in 4 different randomly selected walnut orchards totaling 5.5 ha (3 plots at 46 × 105 m, 4 plots at 50 × 110 m, and 3 plots at 55 × 115 m), with an average of 115.4 trees/ha (s_x = 13.1). Three of the plots were in an isolated orchard surrounded by irrigated pastures, seasonal grasslands, and vineyards; whereas the remaining 7 plots were in orchards within an extensive and continuous orchard landscape. We re-used the same density plots annually at Gray Lodge and Lodi, 1992 through 1995.

We used variably-sized sample plots at Spenceville and Dye Creek. We initially tried 40 × 100 m rectangular survey plots, but this small size could not efficiently capture the widely dispersed nests. Therefore, beginning in 1993 we delineated 20 to 30 separate tracts of Blue Oak woodlands on aerial photographs and randomly selected 6 at each area to be density plots. We replaced 1 plot at Spenceville in 1993 because of a mid-season wild fire, and another because of extensive Poison Oak (*Toxicodendron*

diversilobum) thickets; and we randomly eliminated 1 plot to create a more manageable number. As a result, plot size during 1993 ranged from 3.6 to 13.4 ha and totaled 44.9 ha during the first 3 surveys; 37.7 ha during the 4th survey; and 37.0 ha during the last 3 surveys that year. During 1994 and 1995, plots totaled 36.0 ha, with 3.6 to 8.9 ha in individual plots. Spenceville density plots contained an average of 74.9 Blue Oak trees/ha (s_x = 6.8). At Dye Creek, we used the same plots during 1994 and 1995. The size of 6 individual plots ranged from 4.2 to 10.6 ha and totaled 50.7 ha. Dye Creek plots contained an average of 23.1 Blue Oak trees/ha (s_x = 2.1).

Nest Searches in Plots

We searched for Mourning Dove nests in each density plot during each of the 7 or 8 survey periods every 3rd week. We started each of these tri-weekly surveys on about the same date at all study areas each year, and 21 d separated the average Julian dates of each. We conducted 1 survey during the 2nd week of April (mean Julian date [JD] of 103), 2 in May (JDs of 124, 145), 1 in mid-June (JD = 166), 2 in July (JDs of 187, 208), and 1 in the 3rd week of August (JD = 229) each year; and we added 1 survey in the 1st week of September (JD = 250) at Dye Creek, Spenceville, and Gray Lodge in 1994. Complete coverage of density plots took 1 to 2 d at Gray Lodge and Lodi, and 2 to 4 d at Spenceville and Dye Creek. This schedule adequately covered the most active nesting season, although some early nesting begins in March (Cowan 1952; Miller and others 2001a).

The mean 21-d interval between survey dates reflects the competing needs of obtaining nest density data that would meaningfully index seasonal density trends while minimizing overall disturbance that could deter use by Mourning Doves. Elimination of disturbance in the plots between surveys was of overriding importance (Westmoreland and Best 1985), so we never re-entered plots between survey periods, and all plots were located >100 m from the general nest search areas of the concurrent nesting success field study (Miller and others 2001a). Based on data from Cowan (1952) at Gray Lodge, in which the period from 1st date of egg laying to date of fledglings leaving the nest (a nesting cycle) was 26 to 30 d, the 21-d interval provided a reasonable likelihood that a newly started nest recorded on a given survey would still be active on the succeeding survey, with nestlings ≥7 d old, if the nest survived. In other words, Mourning Doves likely could not complete a full nesting cycle between survey dates, and all successful nests would be counted during at least 1 survey. Some Mourning Doves likely started and lost nests in the plots between surveys; however, we assumed the rate at which this occurred would be similar during and between surveys and among habitats and study areas. Additionally, Mourning Doves usually re-nest in the same general area within a few days to a month (Swank 1955; Mirarchi and Baskett 1994), potentially doing so in the plots.

We methodically searched plots for Mourning Dove nests during each survey by proceeding slowly to cover each plot in its entirety. We thoroughly examined each tree by direct observation and by carefully probing the branches with extendable mirror-poles, which we also used to examine contents of all active nests. We did not actively look for ground nests but recorded them if encountered. We detected nests by sight or when the adult flushed. We defined an active nest as one in which an adult Mourning Dove was present at a nest under construction, with eggs, or with nestlings ≤15 d old, the age of natural fledging (Mirarchi 1993; Mirarchi and Baskett 1994), or one with nestlings even if no adult was present. Once we located a nest, we marked the nest tree, or one nearby, with colored flagging and a small numbered aluminum tag at the tree's base (Miller and others 2001a). We recorded date, parent status (absent, present), nest status (undisturbed, partly destroyed), nest stage (under construction, eggs, nestlings), number of eggs and nestlings, and age of nestlings for each nest to aid record-keeping and identify nests that survived from one survey to the next (Hanson and Kossack 1963). We did not count empty nests if no parent was present.

The project leader (MRM) and field supervisor (CLS) accompanied field technicians on at least 1 d of each survey to ensure consistency in field procedures; however, we suspected that some nests might have been missed (Nichols and others 1986). Therefore, we *a posteriori* estimated the efficiency with which we had detected active nests in the plots. To do this we

counted the number of active nests found on subsequent surveys at each study area that, based on the age of nestlings, should have been located on the previous survey but were not (N_m). We counted the number detected on both the previous and successive surveys (N_d) and calculated nest search efficiency as $N_d \div (N_m+N_d)$.

Statistical Analysis

We estimated Period Nest Density (PND: mean number of all active nests/ha present during any given survey) for each survey by year by study area, by dividing the total number of active nests present in all plots during the survey, whether new or still active from the previous survey, by the respective areas of those plots. We estimated Cumulative Nest Density (CND: total number of different nests found annually/ha) in each plot by year by study area as the sum of the respective PND during all tri-weekly surveys, not including nests recorded on the previous survey. At Spenceville in 1993, because we did not retain all survey plots through the field season, we calculated CND using only the plots for which we obtained data in all 7 periods.

We expected that spring weather would likely influence PND because of the influences of rain and temperature on Mourning Dove nest success in the wider study areas (Miller and others 2001a). We expected habitat type to affect nest density based on previous studies (Cowan 1952; Hanson and Kossack 1963; Sayre and Silvy 1993). We also expected that seasonal survey timing (Geissler and others 1987) and tree density (Sayre and Silvy 1993) would influence PND. Therefore, we constructed a series of candidate models to explain tri-weekly PND at the plot level, and used Akaike's Information Criterion adjusted for small sample size (AIC_C) and Akaike weights to compare candidate models (Burnham and Anderson 2002). We represented spring weather annually by combinations of the temperature and rainfall variables (deviations from average) characteristic of each study area. We designated habitat as a categorical covariate, identified as either riparian, Blue Oaks, or orchard. We considered the possibility that variations in tree density among plots within the same habitat type could influence nesting density. Recognizing that tree density varies with habitat type, we used PROC STDIZE (SAS Institute 2007) to standardize the continuous covariate tree density by habitat type, by subtracting the median tree density to preclude confounding tree density with habitat effects. We used survey wk, numbered tri-weekly from 1 = mid-April through 7 = mid-August (the 8th survey in September 1994 was excluded), and wk^2 to model quadratic nonlinear trends. These models allowed us to evaluate the relative importance of different combinations of habitat (vegetation type and tree density), weather (deviations from average April high temperature and March–May rainfall, and total raindays), and survey timing (survey wk and wk^2). Models with $\Delta AIC_C \leq 2$ are supported, and Akaike weight represents the relative likelihood of models (Burnham and Anderson 2002).

We treated the Mourning Dove nest count from each plot and survey period as a sampling unit for our analyses. Mean nest density equals mean nest count divided by plot size; therefore our models for nest counts are also nest density models. We modeled nest counts as Poisson or negative binomial variables (White and Bennetts 1996) because of their skewed distributions and heterogeneous variances, which increase with mean nest density and plot size. Compared to Poisson distributions, where the ratio c = variance/mean = 1, the negative binomial distribution contains an extra dispersion parameter to estimate $c > 1$ (White and Bennetts 1996; Agresti 2002). The generalized linear mixed model (GLMM) accommodates these distributions, and we applied it to our data using the procedure NLMIXED (SAS Institute 2007). We included fixed effects in all models to explain systematic variations in nest counts resulting from plot size (GLMM offset), habitat, weather, and survey timing (McCullagh and Nelder 1989). Because nest counts are potentially correlated as a result of repeated sampling within study areas, plots, and years, we included random effects to explain variation among random classes (for instance, areas, plots nested in area, years) and intra-class correlations. The GLMM analysis of PND detected zero random effects for study area and year and there was weak to no evidence of over-dispersion (AIC_C was lower for Poisson than for negative binomial models); therefore, we chose Poisson models for our analyses with plot as the only random effect on PND. We analyzed the

TABLE 1. Period Nest Density (PND) (mean nests/ha/survey), Cumulative Nest Density (CND) (total number of different nests recorded/ha), and nest success (Mayfield) (from Miller and others 2001a; Miller MR, unpubl. data for Lodi) of Mourning Doves, in Blue Oak woodlands (Dye Creek, Spenceville), willow-cottonwood riparian woodlands (Gray Lodge), and walnut orchards (Lodi) in the northern Central Valley of California, during warm-dry 1992 and 1994 and cool-wet 1993 and 1995.

Study area	Year	Total plot size (ha)	Number of surveys	Nests	PND	CND	Nest success
Dye Creek[a]	1994	50.71	8[b]	152	0.42	3.00	41.4
	1995	50.71	7	61	0.17	1.20	37.0
Spenceville[c]	1993	40.49[d]	7	28	0.10	0.69	21.5
	1994	36.03	8[b]	54	0.22	1.50	37.9
	1995	36.03	7	19	0.08	0.53	26.9
Gray Lodge	1992	3.52	7	41	1.70	11.65	40.3
	1993	3.52	7	19	0.77	5.40	35.9
	1994	3.52	8[b]	29	1.13	8.24	42.8
	1995	3.52	7	5	0.16	1.42	27.8[e]
Lodi	1992	5.49	7	27	0.70	4.92	38.0
	1993	5.49	7	14	0.36	2.55	24.7
	1994	5.49	7	27	0.70	4.92	22.8
	1995	5.49	7	8	0.23	1.46	19.4

[a] No work was conducted at Dye Creek in 1992 and 1993.
[b] A September survey conducted at Dye Creek, Spenceville, and Gray Lodge in 1994, but data not included in averages in table.
[c] Density not determined at Spenceville in 1992.
[d] Average plot size; see text.
[e] Erroneously reported as 29 in Miller and others (2001a).

relative importance of habitat and weather in relation to CND using the same method as for PND, with the exception that survey timing was no longer of interest because CND was summarized across all survey periods.

To show in a functional way how Mourning Dove nest density likely varied in relation to weather parameters, we regressed average annual PND on average annual rainfall and average annual April high temperature for Gray Lodge, Spenceville, and Lodi (Dye Creek limited to 2 y of data precludes regression) (SAS Institute 2007). We selected among linear (PND = $a + bX$), power (PND = aX^b), exponential (PND = a exp(bX)), and log (PND = $a + b$ log$X$) regressions according to the highest R-square (SAS Institute 2007). The limited number of years of data (3 or 4 per study area) precluded conducting more-complex statistical analyses. We used Fisher's exact test to compare nest search efficiency among study areas. To examine the relationship between nest success and nest density, we regressed nest success estimates, from the nest success study (Miller and others 2001a), on average PND from the present study (SAS Institute 2007).

RESULTS

Validity of Nest Density Estimates

Point estimates of the efficiency of searching for Mourning Dove nests varied among study areas. In walnut orchards at Lodi, we did not find any active nests at a stage of development that indicated we should have detected them on the previous survey but had failed to do so (100% efficiency in finding active nests; N_d = 8 active nests detected in consecutive surveys). In Gray Lodge riparian woodlands, nest search efficiency was 95% (N_m = 1 active nest missed, N_d = 19), and in Blue Oak woodlands search efficiency was 92% at Dye Creek (N_m = 3, N_d = 34), 83% at Spenceville (N_m = 1, N_d = 5), and 91% at Dye Creek and Spenceville combined (N_m = 4, N_d = 39). Despite the differences in point estimates among habitat types, the Fisher's exact test (P = 0.61) suggests these differences likely resulted by chance. Also, the number of active nests missed was relatively small compared to total nests found (76 at Lodi, 94 at Gray Lodge, 101 at Spenceville, and 213 at Dye Creek) (Table 1).

Density Estimates

Period Nest Density generally revealed broadly consistent seasonal patterns of Mourning Dove nesting among study areas, in which PND began low, increased to highs through midsummer, declined toward the end of summer (Fig. 1), and ended before September (based on the September survey in 1994). We recorded 330 active nests during 45 plot surveys

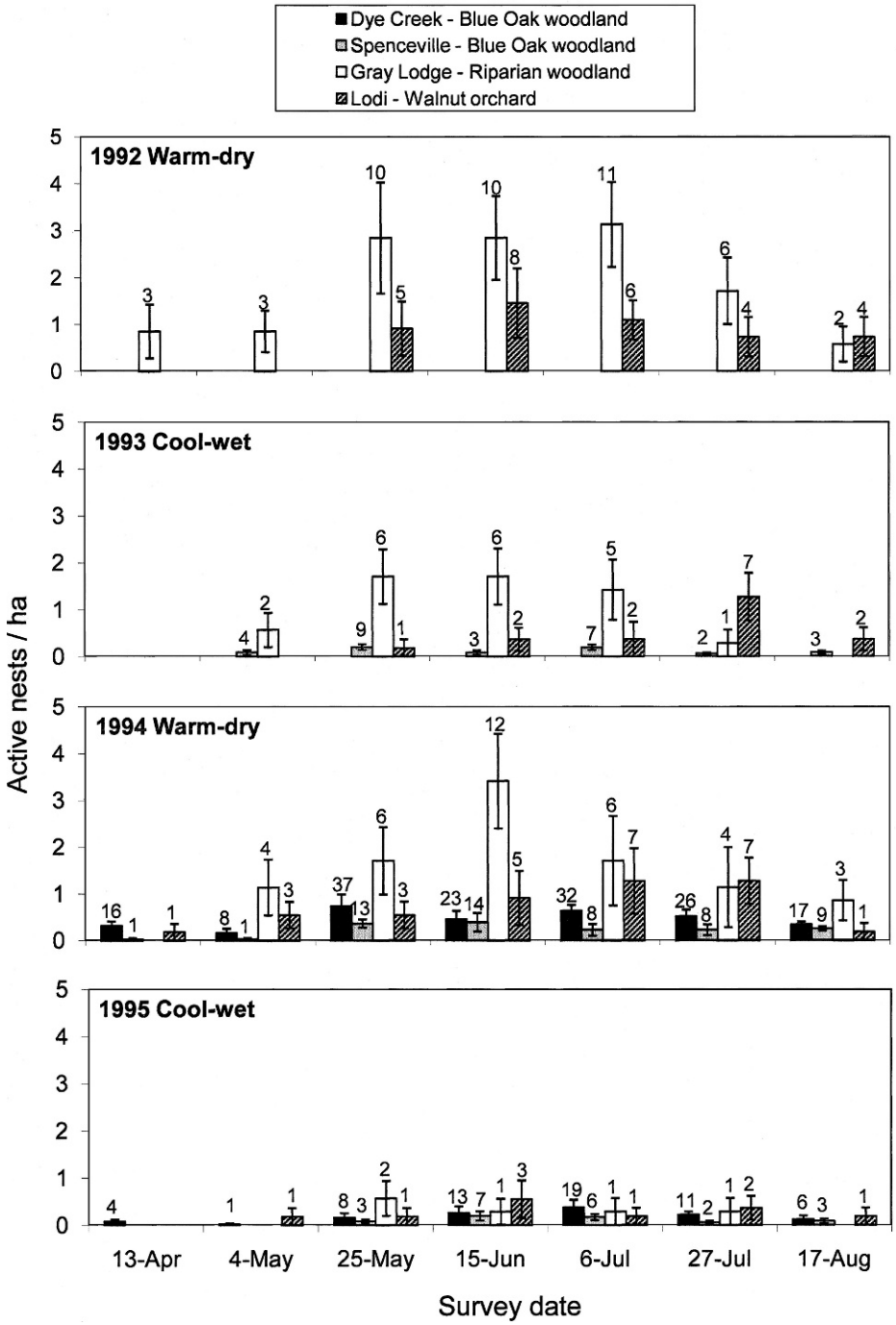

FIGURE 1. Mourning Dove average Period Nest Densities (active nests/ha) (vertical bars), standard errors (vertical lines), and number of nests (numbers above vertical lines) by survey week during mid-April through mid-August of warm-dry (1992, 1994) and cool-wet (1993, 1995) years on 4 study areas in Blue Oak woodlands at Dye Creek Preserve and Spenceville Wildlife Area, in willow-cottonwood riparian woodlands at Gray Lodge Wildlife Area, and in commercial walnut orchards near Lodi in the northern Central Valley, California.

in warm-dry years (including 2 ground nests at Dye Creek in 1994), but only 154 nests during 49 plot surveys in the cool-wet years (Table 1). Likewise, the highest average PND tended to occur during warm-dry years compared to cool-wet years, and PND tended to be relatively much greater in riparian habitat compared to walnut orchards and Blue Oak woodlands in that order, but commonly so only in the warm-dry years (Table 1, Fig. 1). For example, PND in riparian habitat was similar to or less than that of at least 1 other habitat in all surveys during 1995, the coolest and wettest year in our study, and in 3 of 7 surveys in cool-wet 1993 (Fig. 1). The mean PND decreased curvilinearly in response to increasing rainfall, and increased linearly or curvilinearly with increasing April high temperature (Fig. 2).

The data strongly support 2 of our candidate AIC_C models for Mourning Dove PND, as demonstrated by their very small and similar ΔAIC_C and larger weights (Table 2). The best model contains seasonal (wk, wk^2), habitat, temperature and rainfall deviations from average, rain-days, and tree density effects; whereas the 2nd best model is the same but without the rainfall and rain-days effects. The best model (estimate ± SE) predicts PND as:

$$\begin{aligned}\log(\text{PND}) = {} & ß_{\text{veg}} + (1.307 \pm 0.138) \times \text{wk} \\ & - (0.144 \pm 0.016) \times \text{wk}^2 \\ & + (0.305 \pm 0.132) \times \text{temperature} \\ & - (0.053 \pm 0.026) \times \text{rainfall} \\ & + (0.048 \pm 0.030) \times \text{rain days} \\ & - (0.0032 \pm 0.0016) \\ & \times \text{tree density}, \end{aligned} \quad (1)$$

where the intercept $ß_{\text{veg}}$ = −5.234 ± 0.680 for Blue Oak woodlands, −3.609 ± 0.571 for riparian woodlands, and −4.595 ± 0.626 for walnut orchards. The 2nd best model predicts PND as:

$$\begin{aligned}\log(\text{PND}) = {} & ß_{\text{veg}} + (1.307 \pm 0.138) \\ & \times \text{wk} - (0.144 \pm 0.016) \times \text{wk}^2 \\ & + (0.397 \pm 0.083) \times \text{temperature} \\ & - (0.0031 \pm 0.0017) \\ & \times \text{tree density}, \end{aligned} \quad (2)$$

where the intercept $ß_{\text{veg}}$ = −4.354 ± 0.329 for Blue Oak woodlands, −3.011 ± 0.348 for riparian woodlands, and −3.908 ± 0.358 for walnut orchards.

Cumulative Nest Density was highest in the warm-dry years at all study areas and was comparatively the highest in riparian habitat those years (Table 1). The Akaike weights for CND indicated the greatest support for the same habitat and weather variables that we found important for PND, although several simpler models also had support (Table 3). Cumulative Nest Density was best predicted by:

$$\begin{aligned}\log(\text{CND}) = {} & ß_{\text{veg}} + (0.263 \pm 0.135) \\ & \times \text{temperature} - (0.064 \pm 0.027) \\ & \times \text{rainfall} + (0.055 \pm 0.030) \\ & \times \text{rain days} - (0.0032 \pm 0.0017) \\ & \times \text{tree density}, \end{aligned} \quad (3)$$

where the intercept $ß_{\text{veg}}$ = −0.833 ± 0.619 for Blue Oak woodlands, +0.696 ± 0.497 for riparian woodlands, and −0.233 ± 0.559 for walnut orchards.

The relationship between nest density and nest success was mixed among study areas. Nest density correlated positively but weakly with nest success in the walnut orchards (r = 0.67). In contrast, the correlations were strongly positive in the natural habitats (Gray Lodge riparian woodlands: r = 0.94; Dye Creek combined with Spenceville Blue Oak woodlands: r = 0.93; combined Blue Oak and riparian woodlands: r = 0.78) and were curvilinear (the rate of increase in nest success declined as nest density increased) (Fig. 3).

Discussion

Validity of Nest Density Comparisons

We found few active nests that had been active but missed on previous surveys, and there was no statistically significant difference in nest search efficiency among habitat types. Actual nest densities could have been somewhat higher as a result of undetected ground nests. Ground nesting, very common in some regions (Sayre and Silvy 1993; Hughes and others 2000), is rare in the northern Central Valley of California (Cowan 1952; Miller and others 2001a). We did not systematically search for them, and by chance found 2, both in grass among Blue Oaks at Dye Creek. Miller and

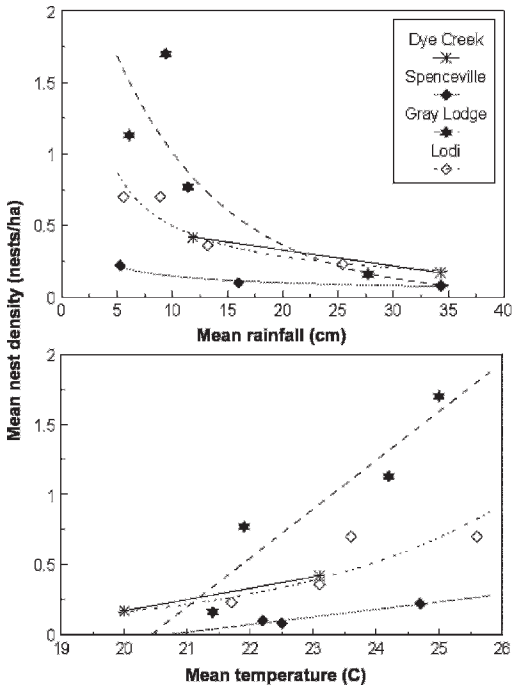

FIGURE 2. Regressions of Mourning Dove average Period Nest Density (PND) on March–May average rainfall and April average high temperature in Blue Oak woodlands at Spenceville Wildlife Area (SP); in willow-cottonwood riparian woodlands at Gray Lodge Wildlife Area (GL); and in commercial walnut orchards near Lodi (LO) in the northern Central Valley, California, 1992–1995. Regression equations for PND on rainfall: $PND_{SP} = 0.53Rainfall^{-0.55}$, $r^2 = 0.96$; $PND_{GL} = 2.81\ exp(-10.0Rainfall)$, $r^2 = 0.90$; $PND_{LO} = 0.99\ exp(-0.06Rainfall)$, $r^2 = 0.90$. Regression equations for PND on temperature: $PND_{SP} = -1.11 + 0.05Temp$, $r^2 = 0.94$; $PND_{GL} = -7.11 + 0.35Temp$, $r^2 = 0.89$; $PND_{LO} = 1.4E-10Temp^{6.94}$, $r^2 = 0.76$. A solid line joins the 2 Dye Creek Blue Oak data points in each graph.

others (2001a) found only 13 ground nests in 4 y among 3417 total nests during the concurrent nest success study, including 5 at Dye Creek, 1 at Spenceville, 7 at Lodi, and 0 at Gray Lodge. We conclude, therefore, that a concerted search effort for ground nests would not change the relative order of nest densities among habitat types, and our data express the inherent habitat differences in Mourning Dove nesting density at a scale consistent with our objectives.

Nest Density

Effects of season.—The seasonal pattern of Mourning Dove nest density in our plots reflected the typical pattern in western North America (Cowan 1952; Geissler and others 1987). This was supported by the quadratic survey week effect with survey timing in our best models. This results from an increasing abundance of nesting Mourning Doves migrating to the region through early summer (Tomlinson 1993; Sayre and Silvy 1993), and the predictable increasing warm-dry weather (Major 1995) that promotes nesting activity (Morrow and Silvy 1982; Miller and others 2001a). Despite this general pattern, annual differences in the initiation of the nesting seasons must have resulted directly from variations in March weather, the proportion of winter resident Mourning Doves in the local populations (Hanson and Kossack 1963), the percentage of Mourning Doves with previous nesting experience (Swank 1955; Armbruster 1983), and the comparative rate of tree foliation (Swank 1955; Schroeder 1970). Additionally, peak and low PND among survey periods often did not occur at the same time among study areas, a common occurrence (Randall 1955; Harris and others 1963; Wolfenden and Rohwer 1969), perhaps resulting from differences in average synchrony of nesting cycles (Wolfenden and Rohwer 1969).

Effects of spring weather.—Cool-wet spring weather caused relatively low PND and CND for Mourning Doves at all study areas compared to the warm-dry years. This is consistent with the suppressive effect of adverse weather on Mourning Dove nest success in the same study areas (Miller and others 2001a), and has been noted elsewhere (Fichter 1959; Hanson and Kossack 1963; Wolfenden and Rohwer 1969; La Perriere 1972; La Perriere and Haugen 1972; Morrow and Silvy 1982; Yahner 1983). Cool-wet weather suppressed the number of pairs and nests, the length of the nesting season, and nest success (Hanson and Kossack 1963; Miller and others 2001a). Apparently, cool-wet weather must have directly delayed nest initiations (Hanson and Kossack 1963; Weeks 1980) or delayed foliation, which indirectly delayed nesting (Fichter 1959; Schroeder 1970). Cool-wet spring weather could also have suppressed early season food supplies. Typically, nesting begins and eggs hatch when food is at peak abundance (Lack 1968:302–304), a pattern suggested for Mourning Doves (Browning 1959), and shown for Wood Pigeons (*Columba palum-*

TABLE 2. The best candidate models (Akaike Information Criterion [AIC_C] < 3 and weights [w] > 0.00) for Mourning Dove Period Nest Density (nests/ha) in the northern Central Valley, California, 1992–1995, in relation to covariates representing: survey timing (wk and wk^2); deviations from April mean high temperature (temp); deviations from mean rainfall (rain) and total rain-days (rain-d) during March–May; habitat (hab); and standardized tree density (treeden). Shown for each model are −2 log likelihood (−2 log L), total parameters (K, including intercept, plot, and variance parameters), AIC_C, differences among AIC_C scores (Δ_C), and Akaike weights (w).

Model	−2 log L	K	AIC_C	Δ_C	w
Wk + wk^2 + hab + temp + rain + rain-d + treeden	1273.77	10	1294.06	0.00	0.25
Wk + wk^2 + hab + temp + treeden	1277.95	8	1294.14	0.08	0.24
Wk + wk^2 + hab + temp + rain + treeden	1276.31	9	1294.55	0.48	0.20
Wk + wk^2 + hab + temp + rain-d + treeden	1277.84	9	1296.08	2.01	0.09
Wk + wk^2 + hab + rain + treeden	1280.10	8	1296.29	2.23	0.08
Wk + wk^2 + hab + temp + rain + rain-d	1278.22	9	1296.45	2.39	0.08

bus) (Murton and others 1963), although disputed by Westmoreland and others (1986). Early nesting Mourning Doves in the northern Central Valley rely on seeds from several annual forbs (Browning 1959, 1962). If cold spring temperature delays flowering and seed production, or previous fall or winter conditions delay sprouting (McClure 1943), Mourning Dove nesting attempts could be delayed until grains and other seeds become available.

The effect of cool-wet spring weather on density measures apparently lasted through the remainder of the weather-shortened nesting seasons (Miller and others 2001a) because PND in cool-wet years was lower than in warm-dry years during all surveys, even in late summer (Fig. 1). We suggest that low temperatures or rain storms in spring may have forced emigration of Mourning Doves or ''short-stopped'' migrants south of northern California. Measureable rainfall in June 1992, 1993, and 1995, rare events (National Oceanic and Atmospheric Administration 1992–1995), could have suppressed summer nests those years; but apparently not enough to change the comparative annual nest densities associated with characteristic weather conditions in spring.

Initially PND declined sharply within the first 10 cm of rain (Fig. 2), but this effect decreased with continued and increasing rainfall. In contrast, PND continued to rise steadily with increasing April high temperatures (Fig. 2). These data suggest that within the range of temperatures and rainfall we encountered, the availability of acceptable nest sites or increasing density-dependent processes (Murton and Isaacson 1964) had not limited Mourning Dove nest density. Therefore, these habitats should be able to accommodate higher Mourning Dove nest densities. Additionally, removing rainfall and rain-days from the best model produced a model essentially as good (Table 2). This stronger support for temperature than precipitation effects in our models probably results from the dominant linear relationship of PND with April high temperatures (Barrientos and others 2007) coinciding with the negative curvilinear relationship of PND and rainfall (Fig. 2), in which

TABLE 3. The best candidate models (Akaike Information Criterion [AIC_C] < 3 and weights [w] > 0.00) for Mourning Dove Cumulative Nest Density (total nests/ha) in the northern Central Valley, California, 1992–1995, in relation to covariates representing: deviations from April mean high temperature (temp); deviations from mean rainfall (rain) and total rain-days (rain-d) during March–May; habitat (hab); and standardized tree density (treeden). Shown for each model are −2 log likelihood (−2 log L), total parameters (K, including intercept, plot, and variance parameters), corrected AIC_C, differences among AIC_C scores (Δ_C), and Akaike weights (w).

Model	−2 log L	K	AIC_C	Δ_C	w
hab + temp + rain + rain-d + treeden	469.00	8	485.91	0.00	0.27
hab + temp + rain + treeden	472.22	7	486.37	1.17	0.15
hab + temp + treeden	474.66	6	486.77	1.58	0.12
hab + rain + rain-d + treeden	472.67	7	486.82	1.63	0.12
hab + rain + treeden	474.71	6	486.82	1.63	0.12
hab + temp + rain + rain-d	473.21	7	487.36	2.17	0.09

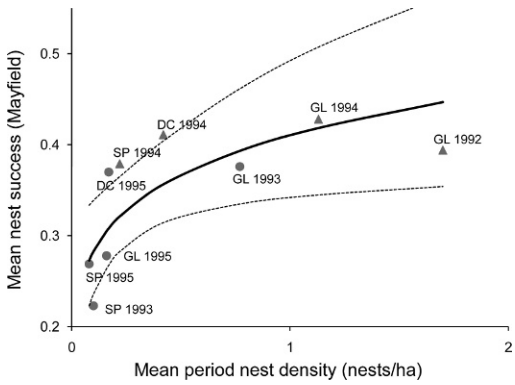

FIGURE 3. Regression of Mourning Dove nest success (Mayfield 1961) from Miller and others (2001a) on Period Nest Density (PND) (this study) in Blue Oak and riparian woodland habitats at combined Dye Creek (DC; Blue Oak woodland), Spenceville (SP; Blue Oak woodland), and Gray Lodge (GL; willow-cottonwood riparian) study areas in the northern Central Valley, California, 1992–95. Nest success = $0.41PND^{0.16}$, with 95% confidence bands based on the model: log(Y) = a + b log(X), where a = −0.89 (SE = 0.08), b = 0.16 (SE = 0.05), and r^2 = 0.60.

rainfall produced diminishing effects on PND as the effects of temperature on PND remained linear. This likely limited the ability of our models to detect the relative effects of rainfall and rain-days at lower nest densities.

Effects of habitat type.—Mourning Dove PND and CND varied by habitat among our study areas, especially in the warm-dry years, with riparian woodlands generally supporting the highest densities. In contrast, Mourning Dove nest success rates tended to be independent of these habitat types during the concurrent nesting success study (Miller and others 2001a), and similar results have been documented by others (Randall 1955; Caldwell 1964; Olson and others 1991; Stoleson and Finch 2001; but see Soutiere and Bolen 1976; Stamp 1978). In Britain, Turtle Dove (*Streptopelia turtur*) populations have declined because of the deterioration of nesting habitat even as nest success has increased (Newton 2004). This supports our conclusion that nest success alone is often not a good predictor of habitat suitability for Mourning Doves. Nest density might fail to predict habitat suitability for birds under certain limited circumstances (Van Horne 1983; Vickery and others 1992), but nest density and success together provide stronger predictions (Johnson 2007). Clearly, for Mourning Doves in our study areas, nest density was better predicted by habitat type than was nest success.

The trend of highest PND and CND of Mourning Doves occurring in riparian habitat was clearly evidenced during warm-dry years but was not consistent during the cool-wet years, especially 1995 when densities in all habitats declined. We speculate that Mourning Doves had reached densities well below the carrying capacity of the habitats, which reflected a weather-induced suppression of nesting effort rather than a reduction in inherent nest capacity of the respective habitats. The top 4 models for PND contained habitat type effects (Table 2), including tree density; so despite supportive or suppressive effects of annual spring weather variables, variation in basic suitability among habitats is a critical determinate of nest density. The negative tree density effect, although quite weak (see best model), reflected a decline in the acceptability of habitats as the more open, edge habitat favored by Mourning Doves (Blue Oak woodlands at Dye Creek, for example) becomes closed and continuous (Spenceville, for example) (Drobney and others 1998).

The way that avian breeding population density relates to nest density has not been explicitly examined in theoretical treatments (Fretwell and Lucas 1970; Van Horne 1983; Bock and Jones 2004; Johnson 2007), but Mourning Doves present a unique problem in this regard. This species undertakes multiple nestings during an extended breeding season (Blockstein and Westmoreland 1993), so the cumulative number of nests greatly exceeds the nesting pairs. The metric used to monitor breeding population density, the number of doves heard calling (Dolton 1993), does not usually correlate with the number of Mourning Doves actually nesting because unmated males call more frequently than mated males and only the latter build nests (Baskett 1993). Therefore, data on nest density could better index habitat quality for nesting Mourning Doves than would breeding-population density, more directly supporting conservation of habitats that recruit the greatest number of young into breeding populations (Bock and Jones 2004).

Nest success and nest density.—Van Horne (1983) suggested that population density alone could be a misleading indicator of habitat

suitability if there was a negative correlation between population density and reproductive success (or survival). The nesting data for Mourning Doves (Miller and others 2001a), however, suggest that nest success can also be a misleading indicator of habitat quality. Allee and others (1949) proposed that nest success should increase with population size (density) up to some maximum, but thereafter decline with further increases in density associated with, for example, increased competition for resources or increased predation (Fretwell and Lucas 1970). Bock and Jones (2004), however, reviewed numerous studies and found that the overwhelming majority (72%) of those conducted in intact habitats showed positive correlations between avian breeding population density and nesting success (recruitment per capita). They also found that the density of breeding adults was a major contributor to the number of young produced per unit area, and that density was usually more important than nest success in indexing habitat quality (Bock and Jones 2004). Therefore, biological factors that allow nest density to increase should allow nest success to increase (Fichter 1959; Bock and Jones 2004), at least within some threshold (Allee and others 1949).

The curvilinear relationship between nest success and nest density in riparian and Blue Oak woodlands suggests that increases in Mourning Dove nest success might be limited by density-dependent factors as nest density increases, such as disproportionate increases in the loss of nests to predation or food shortages. Our data show no evidence of limits to nest density within the ranges we recorded. Nest success (Miller and others 2001a), however, neared a plateau of about 0.5 (calculated from nest exposure days; Mayfield 1961) even as average nest density showed no evidence of being constrained (Fig. 3). Mourning Dove nest success is likely correlated to the stability of nest supports, such as robust branch structure, underlying their generally flimsy nests (Coon and others 2001). Therefore, nest density by habitat type could primarily reflect the comparative availability of acceptable nest sites in the characteristic trees or other vegetation (McClure 1943; Jumber and others 1956; Hanson and Kossack 1963; Caldwell 1964; Wolfenden and Rohwer 1969; Yahner 1982); and any limits to Mourning Dove nest density resulting from this inherent habitat capacity obviously had not been reached during our study. We suspect that Mourning Dove nest density increased unconstrained under warm-dry conditions, which likely reflected the wide availability of acceptable trees with suitable branch structure to support nests, and declined during the cool-wet conditions even though the habitat features supporting nests were still present. It follows that the steady increase of nest density concurrent with the declining rate of increase of nest success is evidence that nest density was more characteristic of the studied habitats than was nest success, at least at the low to moderate nest densities we encountered.

Territoriality in birds can play a role in population density (Fretwell and Lucas 1970; Goforth and Baskett 1971); however, Mourning Doves defend small territories that only include cooing perches and the source of nest building materials (Sayre and Silvy 1993; Sayre and others 1993). Additionally, once a nest is established territorial defense ceases and additional dove pairs can nest nearby without conflict, including in the same tree (Sayre and Silvy 1993), and Mourning Doves can nest in a semi-colonial state (2.5 to 7.4 pairs/ha; Irby 1964). Bock and Jones (2004) found that 86% of studies showed positive correlations between nest density and success for such weakly territorial species. Therefore, the potential for territoriality to limit nest density in Mourning Doves is likely small in the habitats we studied.

Additional research.—The fundamental relationship between nest success and nest density by habitat type has not been intensively studied in Mourning Doves. Obtaining such data should be of interest because the suitability of each habitat is related to its contribution to the gene pool of the species (Fretwell and Lucas 1970), and this could be primarily a function of nesting density (Bock and Jones 2004). Riparian vegetation tends to support a high density of Mourning Dove nests, and the Blue Oak woodlands encircling the Sacramento Valley constitutes a large proportion of available natural Mourning Dove nesting habitat in California (Drobney and others 1998). Researchers should intensify investigations to identify the key features of these and orchard habitats required by nesting Mourning Doves, and

determine how Mourning Dove nesting behavior in these habitats interacts concurrently with spring weather to regulate Mourning Dove nesting habitat selection, nest density, nest success, production of young, survival of adults and immatures (Johnson 2007), and ultimately, population size. Development of indices of nest density should be useful in assessing responses of nesting Mourning Doves to local weather, available nesting habitats, and habitat restoration programs.

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