

LATE SUMMER AND FALL NESTING IN THE ACORN WOODPECKER AND OTHER NORTH AMERICAN TERRESTRIAL BIRDS

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Abstract. Acorn Woodpeckers (*Melanerpes formicivorus*) at Hastings Reservation in central coastal California exhibit a bimodal peak in annual breeding activity. One peak occurs in spring during which the majority of breeding takes place, while a second is centered in late August as the new acorn crop matures. These latter nests are mostly initiated in late summer but often do not fledge until at least late September and are thus referred to here as ‘fall’ nests. Fall nests occur in about one-third of all years, taking place when the acorn crop is large and summer temperatures are relatively high. Fledglings from fall nests constitute 4.3% of the population’s total productivity and survive and recruit to the population at levels comparable to spring fledglings. Fall nesting is less likely in groups in which either the male or female breeding adults have undergone a change from the prior year, but groups are otherwise indistinguishable. Ecologically, fall nesting is closely tied to the acorn crop and thus to breeding success in the following, rather than the prior, spring. Among North American terrestrial birds in general, fall breeding has been reported in 16% of all species and is significantly more common among residents and colonially nesting species, in which the frequency exceeds 25%. Furthermore, fall nesting is likely to have been underreported in the literature. Thus, this phenomenon is at least an irregular part of the breeding biology of a substantial fraction of North American birds and should be considered a possibility in population studies of temperate-zone species. This is especially true given that fall nesting is likely to increase as global warming takes place.

Key words: Acorn Woodpecker, autumnal breeding, breeding phenology, demography, late nesting, *Melanerpes formicivorus*.

Nidificación a Fines del Verano y Durante el Otoño en *Melanerpes formicivorus* y Otras Aves Terrestres Norteamericanas

Resumen. En la Reserva Hastings de la costa central de California, el carpintero *Melanerpes formicivorus* exhibe un patrón bimodal en su actividad reproductiva anual. Un pico durante el cual ocurre la mayor parte de la actividad reproductiva tiene lugar en la primavera, mientras que un segundo pico se presenta a fines de agosto, cuando las bellotas comienzan a madurar nuevamente. Estos últimos nidos son iniciados en su mayoría a fines del verano y en la mayoría de los casos los polluelos no abandonan el nido hasta fines de septiembre, por lo que a estos nidos los llamamos nidos de ‘otoño’. Los nidos de otoño son observados en aproximadamente un tercio de los años, y se presentan cuando la producción de bellotas es alta y las temperaturas durante el verano son relativamente altas. Los polluelos que provienen de nidos de otoño constituyen el 4.3% de la productividad total de la población y sobreviven y se incorporan a la población a tasas similares a las de los polluelos de primavera. La probabilidad de que ocurra nidificación de otoño es menor en grupos en los que el macho o la hembra de una pareja reproductiva han cambiado con respecto al año anterior, pero en otros aspectos dichos grupos no pueden distinguirse. Ecológicamente, la nidificación de otoño se relaciona fuertemente con la producción de bellotas y por ende con el éxito reproductivo del año siguiente y no con el de la primavera anterior. En general, entre las aves terrestres de Norteamérica, se ha reportado que el 16% de todas las especies exhiben nidificación de otoño, y que este comportamiento es significativamente más común entre las aves residentes y las que nidifican en colonias, grupos en los cuales la frecuencia de nidificación de otoño excede al 25%. Además, es probable que la nidificación de otoño haya sido subestimada en la literatura. Por esta razón, al menos de forma irregular, este fenómeno es parte de la biología reproductiva de una fracción importante de las aves de Norteamérica, y debería ser considerado como una posibilidad

en los estudios poblacionales de las especies de zonas templadas. Esto es especialmente importante ya que la nidificación de otoño probablemente aumentará con el calentamiento global.

INTRODUCTION

Of the various facets of the breeding biology of North American birds, the distribution of nesting within the breeding season, including the frequency and potential for late summer and fall nesting, is one of the least well known. These late nests will, for simplicity, be referred to subsequently as 'fall' nests. The reason for this is no mystery: in temperate climates most breeding takes place in the spring and summer. Thus, little attention generally has been devoted to the possibility of fall nesting. It has, however, been recognized for over half a century that many resident species experience a period of active sexual behavior in the fall, at which time the gonads enlarge and some individuals may achieve spermatogenesis (Marshall 1952, 1959). Furthermore, records of autumnal breeding have been scattered throughout the literature for years. For example, unusually large numbers of nests were observed for at least seven species in Britain during November–December 1953 (Snow 1955), and Orians (1960) briefly summarized records of fall nesting for 11 species in California in his discussion of the phenomenon in Tricolored Blackbirds (*Agelaius tricolor*). In both of these cases, fall nesting was attributed to environmental conditions, particularly relatively mild temperatures. However, the extent and causes of fall breeding remain to be determined for the majority of temperate species.

Here we examine in detail the phenomenon of fall breeding in the Acorn Woodpecker (*Melanerpes formicivorus*), a species highly dependent on acorns that sometimes breeds in the late summer and fall in California (Koenig, Stacey et al. 1995). In particular, we expand on an earlier discussion of fall nesting in this species (Koenig and Mumme 1987) by analyzing the factors responsible for the occurrence and frequency of fall nesting as well as the fate of fall fledglings. We also compile a list of fall nesting records for North American terrestrial birds, with the aim of encouraging greater attention to documenting the distribution of breeding attempts of North American birds and increasing awareness of the potential for

breeding outside the 'usual' spring and early summer season.

METHODS

ACORN WOODPECKER STUDY

Acorn Woodpeckers are cooperative breeders that have been continuously studied at Hastings Reservation, Monterey County, California, since 1972 (MacRoberts and MacRoberts 1976, Koenig and Mumme 1987). Throughout this long-term study, we have attempted to find all nesting attempts by the individually color-marked population of between 25 and 50 resident groups over an area of approximately 300 ha; nests followed between fall 1974 and fall 2005 are included in the analyses performed here (31 complete years plus fall 1974). Although a few nesting attempts were missed, even in spring, our continuous surveys of the population confirm that this was invariably a small proportion of successful nests. Because egg-laying is in some cases a protracted affair involving egg destruction by joint-nesting females (Koenig, Mumme et al. 1995), we report estimated or known last egg date rather than the more commonly used first egg date. Sample sizes sometimes vary among analyses depending on the precise sample of nests and groups for which relevant information was known.

Between 1972 and 2005 the fate of 3194 birds banded as nestlings was determined. We compared the success of spring vs. fall fledglings in two ways. First, we compared the overall proportion of fledglings that was seen after banding, the proportion that survived to their first February, the proportion that eventually became breeding adults somewhere within the study area, and the sex ratio of spring vs. fall fledglings. Although many offspring, particularly females, emigrate out of the study area (Koenig et al. 2000), dispersal rarely occurs prior to the first spring; thus, fledglings that disappeared prior to their first March were assumed to have died. The sex of fledglings generally cannot be determined without molecular analyses until the postjuvenile molt, which takes place 3–4 months after fledging, or around September for spring nestlings (Spray

and MacRoberts 1975). Thus, except for a small number of birds that were sexed using molecular techniques for another study (Koenig et al. 2001), most nestlings were not sexed unless they survived for several months after fledging.

The second way we tested the success of fall fledglings controlled for annual differences by comparing the survivorship and fate of fledglings for each year in which fall nesting occurred. We then contrasted the success of spring vs. fall nestlings using sign tests. Sample size included the 10 years between 1975 and 2005 in which fall nesting took place (two fall nests are also known to have been attempted in 1974, but this year was excluded from analysis due to a lack of detailed information on the population at that time). Results of the two sets of analyses were essentially the same, thus only results from the prior analysis are presented.

Previous work has indicated that the size of the acorn crop is critical to both overwinter residency and reproductive success, including fall nesting, of Acorn Woodpeckers (Hannon et al. 1987, Koenig and Mumme 1987). Partly in response to this apparent dependency, we initiated an ongoing acorn survey in the study area in 1980 (Koenig, Knops et al. 1994, Koenig, Mumme et al. 1994). The survey consists of two individuals each counting as many acorns as possible within 15 sec (30 sec total) on 250 marked oaks (subsequent tree mortality has decreased this number somewhat) divided unevenly among the five species common within the study area (valley oak [*Quercus lobata*], 88 trees; blue oak [*Q. douglasii*], 57 trees; canyon live oak [*Q. chrysolepis*], 21 trees; coast live oak [*Q. agrifolia*], 63 trees; and California black oak [*Q. kelloggii*], 21 trees). As an index of the acorn crop each fall between 1980 and 2005, we used the mean number of acorns counted in 30 sec across all trees surveyed that fall.

Variables examined for their relationship with fall nesting activity included the overall size of the acorn crop, reproductive success of the population the prior spring, and environmental conditions, specifically weather conditions during August and September, the period of fall nest initiation, and the amount of rainfall during the prior year (September–August), the latter of which falls almost entirely between November and March in the Mediterranean climate of the study area. Tests were performed

to contrast years when fall nesting did and did not take place and to explain overall fall nesting activity measured as fall nests per group. Univariate tests were nonparametric (Mann-Whitney *U*-tests and Spearman rank correlations). Multivariate tests included logistic regression (for the dichotomous variable of whether fall nesting occurred or not) and stepwise multiple regression to compare variables potentially influencing the rate of fall nesting.

We tested for factors facilitating fall nesting in years when it occurred by performing Wilcoxon signed-ranks tests comparing groups that were known to have fall nests in those years vs. groups that did not. As before, sample size included the 10 years between 1975 and 2005 in which fall nesting took place. Parameters tested included group composition (number of breeding adults, number of helpers, total group size), spring reproductive success (number of successful nests, number of young fledged, number of young surviving to 1 August of their first year), and whether there had been a change (turnover) in either the male or female breeding adults since the previous year.

REVIEW OF AUTUMNAL BREEDING IN NORTH AMERICAN TERRESTRIAL BIRDS

Our primary source for information on fall nesting was the recently completed *Birds of North America* series. However, additional nesting records were gleaned from the literature and solicited via society newsletters. We also included records of fall clutches from the Western Foundation of Vertebrate Zoology that had been entered into a computerized database as of July 2006 (approximately 30% of their collection). We restricted our search to terrestrial species (i.e., excluding waterbirds and shorebirds) breeding at least partly within North America north of Mexico. Hawaiian and extinct (or nearly extinct) species were not included. We included introduced species as long as some information existed on breeding phenology within North America. Our goal was to be comprehensive, but a number of more obscure records of fall nesting were almost certainly missed.

As an operational definition of fall nesting we included cases in which eggs were laid or incubation was observed between 1 September and 30 November. This arbitrary definition was

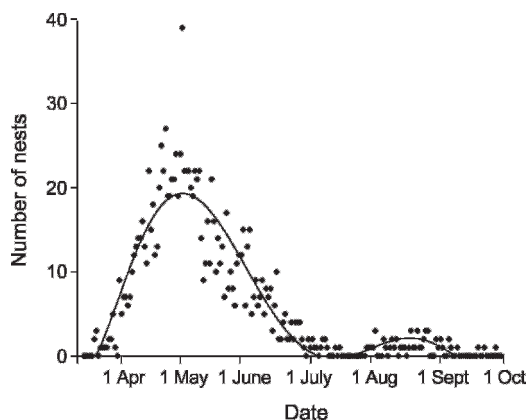


FIGURE 1. The temporal distribution of last egg dates for 1173 nests of Acorn Woodpeckers at Hastings Reservation, California, between 1974 and 2005. Line drawn by eye. Note the bimodal distribution with the primary peak centered around 1 May for spring nests and the much smaller secondary peak centered in mid-August for fall nests.

made necessary by the lack of detailed nesting phenology for most species combined with the desirability of using a common definition for all species considered in the analysis.

Two life-history variables were tested for their relationship with fall nesting. The first was migratory status (primarily migratory, primarily resident, or intermediate, with the last category including species that are nomadic, partially migratory, or exhibit seasonal movements), and the second was nest spacing (primarily solitary or primarily colonial or semicolonial). Information on these characters was obtained from the *Birds of North America* series and Ehrlich et al. (1988).

RESULTS

FALL NESTING IN THE ACORN WOODPECKER

Between fall 1974 and fall 2005 we recorded the estimated or known last egg date for 1173 nests (Fig. 1). The range in estimated last egg dates was 20 March to 27 September, or 191 days. However, the distribution was bimodal, with a strong peak in spring around 1 May and a weak secondary peak around mid-August. In between the two peaks was a 12-day lull from 16–27 July during which no nests were initiated. Consequently, we defined fall nests as those occurring within the range of the secondary peak, including all nests following the 12-day

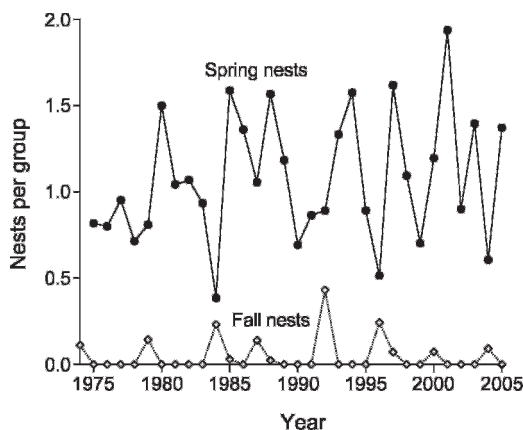


FIGURE 2. The frequency of spring and fall nests by year for Acorn Woodpeckers at Hastings Reservation from fall 1974 to fall 2005, measured as the number of nests group⁻¹. Although fall nests occur in only one-third of years and are generally rare, in some years (i.e., 1984, 1992, and 1996) a substantial fraction of the population's annual productivity can come from fall nests.

lull in nesting activity ending on 27 July. Nests with last egg dates prior to 16 July are referred to as spring nests. Of the 1173 nests, 51 (4.3%) were fall nests by the above definition. A total of 137 young was banded at these nests, amounting to 4.3% of all young banded over the course of the study.

Fall nests were recorded in 11 of 32 years (34%). Standardized by the number of groups being studied at the time, the incidence of fall nesting ranged up to 0.43 group⁻¹. By comparison, spring nests ranged from a low of 0.39 group⁻¹ in 1984 to a high of 1.93 group⁻¹ in 2001 (Fig. 2). These latter values include renesting attempts and any second nests with last egg dates prior to 16 July; no renesting or second attempts during the fall season were detected during the study. In terms of number of young fledged within a year, fall nests on average contributed 9% of annual productivity overall and 19% of young in years when fall nesting occurred. Fall nests contributed 39% of all fledglings produced by the population in 1996 and 50% in 1984.

In both the univariate and multivariate analyses the occurrence and frequency of fall nesting correlated positively with a larger acorn crop and with warmer maximum summer temperatures (Table 1). There was no signifi-

TABLE 1. Results of tests examining whether certain factors influenced whether or not fall nesting occurred in Acorn Woodpeckers at Hastings Reservation during a particular year and whether they affected the incidence of fall nesting measured as the number of nests group⁻¹. Number of years are given in parentheses. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; other $P > 0.05$.

Variable	Whether fall nesting occurred or not		Rate of fall nesting	
	Mann-Whitney U-test (z-value)	Logistic regression (Wald statistic; df = 1)	Spearman rank correlation (r_s)	Stepwise multiple regression (t-value)
Mean acorn crop	3.3*** (26)	5.5*	0.66*** (26)	2.4*
Spring nests per group	0.4 (31)	0.1	-0.20 (31)	1.7
Annual rainfall	0.8 (32)	0.1	-0.08 (32)	0.3
Mean minimum summer temperature	1.6 (32)	0.3	0.35* (32)	1.2
Mean maximum summer temperature	2.5* (32)	3.8*	0.49** (32)	3.4**
Overall model	—	$\chi^2_2 = 21.1***$	—	$F_{2,23} = 9.5***$

cant relationship with either annual rainfall or the number of spring nests per group.

Although there was no relationship between spring and fall nests within the same year, there was a highly significant positive correlation between the incidence of fall nesting and spring nesting activity the following year (Fig. 3). This highlights the common ecological basis of nesting activity during these two periods, both of which are strongly influenced by the fall acorn crop.

We also compared composition and several other group characteristics between groups with and without fall nests in the 10 years when fall nesting took place. The only significant differ-

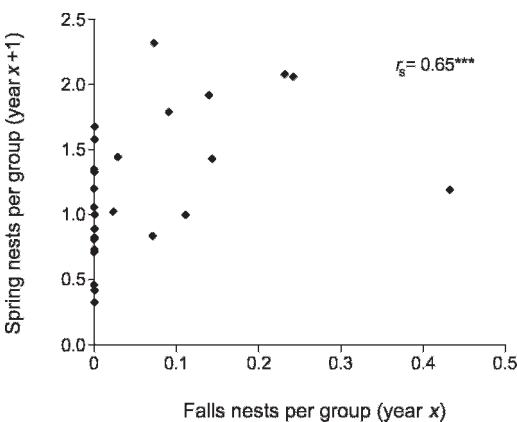


FIGURE 3. The number of fall nests per group (year x) was positively correlated with the number of spring nests per group the following year (year $x + 1$) for Acorn Woodpeckers at Hastings Reservation between 1974 and 2004 ($n = 31$ years), showing their common dependence on the acorn crop in fall of year x .

ence that emerged was that groups undergoing a turnover from the prior year were less likely to have a fall nest than groups whose breeding composition was unchanged (Wilcoxon signed-ranks test, $z = 2.0$, $P < 0.05$; all other comparisons $P > 0.5$).

Among fledglings surviving long enough to be sexed on the basis of plumage characteristics, there was no difference in sex ratio between seasons (895 of 1652 [54%] sexed spring fledglings were males vs. 48 of 84 [57%] sexed fall nestlings; $\chi^2_1 = 0.3$, $P = 0.6$). We also detected no significant difference in survivorship between spring and fall fledglings when measured as whether nestlings were seen out of the nest after banding or not (2165 of 3057 [71%] spring nestlings were seen after banding vs. 98 of 137 [72%] fall nestlings; $\chi^2_1 = 0.03$, $P = 0.9$), or as the eventual probability of spring vs. fall nestlings becoming breeding adults within the study area (593 of 2721 [22%] spring fledglings vs. 25 of 129 [19%] fall nestlings became breeders; $\chi^2_1 = 0.4$, $P = 0.5$; analyses restricted to young fledged in 2002 or earlier).

We found a significant difference in the probability of spring vs. fall fledglings surviving to their first February (1379 of 3057 [45%] spring nestlings vs. 84 of 137 [61%] fall nestlings survived to February; $\chi^2_1 = 13.9$, $P < 0.001$). However, given that spring nestlings had to live on average several months longer than fall nestlings in order to still be present the following February, the biological significance of this difference is unclear. It does, however, support the conclusion that fall fledglings survive at least as well as spring nestlings.

AUTUMNAL BREEDING IN NORTH AMERICAN TERRESTRIAL BIRDS

Our survey of North American terrestrial birds revealed evidence for fall nesting in 69 species (Table 2), or 16% of the 441 species surveyed. Three of these species (Snail Kite [*Rostrhamus sociabilis*], Bald Eagle [*Haliaeetus leucocephalus*], and Crested Caracara [*Caracara cheriway*]), regularly initiate breeding in the winter and occasionally start as early as the fall. The remaining 66 species breed primarily in the spring and summer. All records are for North America with the exception of those for the Common Raven (*Corvus corax*), which is included based on three records from Scotland (Mearns and Mearns 1989).

Dividing species according to their migratory status (Table 3) confirmed that residents exhibit fall nesting at significantly higher rates than do primarily migratory species (Fisher exact test, $P < 0.001$). However, migrating over long distances does not preclude fall nesting, as demonstrated by the 11 species of migrants, including several that migrate to the Neotropics, for which fall nesting has been documented. The difference between the incidence of fall nesting among resident species and those that are intermediate between resident and fully migratory species was marginal (Fisher exact test, $P = 0.15$; $P = 0.04$ if the three species that were intermediate overall but known to be resident in the locality where fall nesting was reported were included as residents). Excluding fully migratory species, records of fall nesting were found in 58 of 230 (25%) species.

Of the species surveyed, 64 nest colonially or semicolonially (Table 3). Of these, fall nesting has been detected in 17 (27%), significantly greater than the proportion of fall-nesting species among solitary nesting species (Fisher exact test, $P = 0.02$).

DISCUSSION

Late summer and fall nesting, corresponding with the maturation of the fall acorn crop, is an irregular but important part of the breeding biology of Acorn Woodpeckers in central coastal California. Over the period of our study, 4.3% of fledglings came from such nests. However, in some years, fall nesting contributes a much higher proportion of young fledged, amounting to at least 10% in six of 31 years and ranging as high as 50% in 1984. Fall fledglings

survived as well and were just as likely to be recruited to the population as spring fledglings.

As proposed earlier (Koenig and Mumme 1987), fall nesting was significantly correlated with larger acorn crops. Acorns are fed to nestlings and, more importantly, form a large portion of the diet of adults feeding nestlings (WDK, unpubl. data). Thus, the finding that larger acorn crops facilitate fall nesting is not surprising. Less expected was the importance of warmer summer temperatures, the effect of which was comparable in magnitude to that of the acorn crop. Whether this is because warmer summer conditions facilitate greater insect abundance during this period or because warm weather decreases the thermoregulatory demands of the birds (Weathers et al. 1990) is unknown.

Ecologically, fall nesting in year x is related not to the (earlier) year x spring breeding season but rather to the spring breeding season the following year (year $x + 1$), events both linked to the year x acorn crop (Koenig and Mumme 1987). Thus, rather than claiming that the breeding season of Acorn Woodpeckers (as indexed by the last egg date) at our study site extends from 20 March to 27 September, a period of 192 days with a short 12-day lull from 16 to 27 July, it is ecologically more valid to say that the breeding season starts with fall nesting on 28 July and extends until 15 July the following year, a period of 353 days interrupted by a 174-day winter lull (28 September to 19 March) during which no nests are initiated. A comparable argument could be made for other species, including Western Scrub-Jays (*Aphelocoma californica*), Pinyon Jays (*Gymnorhinus cyanocephalus*), and crossbills (*Loxia* spp.), whose fall breeding behaviors are related to fall seed crops whose ecological effects are likely to be exerted on the subsequent, rather than the prior, spring breeding season. To the extent this is true, fall nesting in these species starts, rather than ends, the breeding season.

Our survey of North American terrestrial bird species confirms that fall nesting is more widespread than generally appreciated. Of 441 species surveyed, we found evidence for egg-laying in September–November, our criterion for fall nesting, in 69, or 16%. Fall-nesting species were widely distributed taxonomically and included species from nine of 13 (69%) orders and 24 of 47 (51%) families, including 13

TABLE 2. Summary of fall nesting records for North American terrestrial birds.

Species	Migratory status (coloniarity) ^a	Evidence ^b	Notes	Reference
Snail Kite (<i>Rostrhamus sociabilis</i>)	Resident (C)	Clutches initiated all months of year (FL)	Breeds in winter; breeding related to water levels	Sykes (1987)
Golden Eagle (<i>Aquila chrysaetos</i>)	Partial migrant	Four clutches collected 17 Sept.–24 Nov. (CA; CO; MT)		WFVZ ^c
Bald Eagle (<i>Haliaeetus leucocephalus</i>)	Variable	Incubation as early as Oct. (FL)		Broley (1947)
Harris's Hawk (<i>Parabuteo unicinctus</i>)	Resident	Nests every month of year (AZ)	Breeds in winter	Bednarz (1987)
Osprey (<i>Pandion haliaeetus</i>)	Mostly migratory (C)	Four clutches collected 5 Oct.–5 Dec. (NY)		WFVZ
Crested Caracara (<i>Caracara cheriway</i>)	Resident	Earliest nests in Sept. (FL; AZ)	Breeds in winter, coinciding with the dry season	Morrison (1996); WFVZ
Peregrine Falcon (<i>Falco peregrinus</i>)	Variable	Replacement clutches as late as Sept. (CA)		White et al. (2002)
Plain Chachalaca (<i>Ortalis vetula</i>)	Resident	Hatching as late as Sept.–Oct. (TX)		Marion and Fleetwood (1978)
Scaled Quail (<i>Callipepla squamata</i>)	Resident	Clutch hatched 22 Sept. (NM)		Jensen (1925)
California Quail (<i>Callipepla californica</i>)	Resident	Hatching as late as early Sept. (CA); one clutch collected 21 Sept. (CA); 10-day-old young seen 10 Jan. (CA)		Compton (1931); Calkins et al. (1999); WFVZ
Gambel's Quail (<i>Callipepla gambelii</i>)	Resident	Hatching as late as Sept. (NM)		Raitt and Ohmart (1966)
Northern Bobwhite (<i>Colinus virginianus</i>)	Resident	Not unusual for birds to hatch as late as Oct. (Nov. in S. TX)		Brennan (1999)
Montezuma Quail (<i>Crytonyx montezumae</i>)	Resident	Hatching through Sept. (AZ)		Willard (1913); Stromberg (2000)
Rock Pigeon (<i>Columba livia</i>)	Resident (C)	Breeds year round	Introduced	Johnston (1992)
Band-tailed Pigeon (<i>Patagioenas fasciata</i>)	Partial migrant	Nest found with fresh eggs as late as 25 Oct. (AZ)	Possibly linked to the acorn crop	Phillips et al. (1964); Gutiérrez et al. (1975); Keppie and Braun (2000)
White-crowned Pigeon (<i>Patagioenas leucocephala</i>)	Resident (C)	3 of 499 clutches (0.6%) laid in Sept. (FL)	Bimodal nesting season. Proportion nesting in later period and in a given year related to fruit supply	Bancroft et al. (2000); Bancroft and Bowman (2001)
Eurasian Collared-Dove (<i>Streptopelia decaocto</i>)	Resident	Nests every month but January (FL)	Introduced	Stevenson and Anderson (1994); McNair (1997)

TABLE 2. Continued.

Species	Migratory status (coloniality) ^a	Evidence ^b	Notes	Reference
Spotted Dove (<i>Streptopelia chinensis</i>)	Resident	Juveniles with unsheathed flight feathers 31 Oct. (CA); nest-building in Dec. (CA)	Introduced. Breeds virtually throughout the year in S. CA	Baptista (1976); Garrett and Walker (2001)
Mourning Dove (<i>Zenaidura macroura</i>)	Mostly resident	10% of young fledge Sept.-Oct.		Sayre and Silvy (1993)
Inca Dove (<i>Columbina inca</i>)	Resident	Breeds to late Dec. (TX) and to Nov. (AZ)		Phillips et al. (1964); Oberholster (1974)
Common Ground-Dove (<i>Columbina passerina</i>)	Resident	Nests initiated early Feb. through early Oct. (FL)	Seasonal peaks may coincide with seed production	Bowman and Woolfenden (1997)
Monk Parakeet (<i>Myiopsitta monachus</i>)	Resident (C)	Second clutch laid 1-5 Sept. (IL)	Introduced. Late nests suggested to be a holdover from S. American origin	Neidermeyer and Hickey (1977)
Black-billed Cuckoo (<i>Coccyzus erythrophthalmus</i>)	Migrant	Eggs found on 14 Sept. (MI)	Dependent on erratic insect outbreaks	Bent (1940); Pistorius (1985)
Yellow-billed Cuckoo (<i>Coccyzus americanus</i>)	Migrant	Second clutch begun in Sept. (KY)	Dependent on erratic insect outbreaks. Late nests in all parts of range	Mengel (1965); Hughes (1999)
Smooth-billed Ani (<i>Crotophaga ani</i>)	Resident	Eggs from third broods laid 15 Aug.-16 Sept. (FL)		Loflin (1983)
Barn Owl (<i>Tyto alba</i>)	Resident	Clutches initiated Jan.-Oct. (TX); hatching as late as 4 Oct. (UT)	Breeding dependent on rodent populations	Otteni et al. (1972); Baudvin (1975); Marti (1994)
Burrowing Owl (<i>Athene cunicularia</i>)	Partial migrant; resident in FL (C)	Breeding can start as early as Oct. (FL); clutch laid in Oct., hatched in Nov. (AZ)		Millsap and Bear (1990); C. Conway, Univ. Arizona, pers. comm.
Buff-bellied Hummingbird (<i>Amazilia yucatanensis</i>)	Resident	Two nestlings in Oct. (TX)		Chavez-Ramirez and Moreno-Valdez (1999)
Ruby-throated Hummingbird (<i>Archilochus colubris</i>)	Migrant	Eggs found 2 Sept. (ON)		Peck and James (1983)
Anna's Hummingbird (<i>Calypte anna</i>)	Mostly resident	Nestlings on 16 Nov. (AZ)	Late nests possibly related to exotic flowering plants	Witzeman (1984)
Lewis's Woodpecker (<i>Melanerpes lewis</i>)	Irregular; some seasonal movement (C)	Nest with young 29 Sept. (WA)		Jewett et al. (1953); Bock (1970)

TABLE 2. Continued.

Species	Migratory status (coloniality) ^a	Evidence ^b	Notes	Reference
Acorn Woodpecker (<i>Melanerpes formicivorus</i>)	Resident	Last egg date as late as 27 Sept. (CA)		This study
Northern Beardless-Tyrannulet (<i>Camptostoma imberbe</i>)	Resident	Incubation as late as 6 Sept. (TX)		Brush (1999)
Eastern Wood-Pewee (<i>Contopus virens</i>)	Migrant	Eggs as late as mid-Sept. (OH)		McCarty (1996)
Black Phoebe (<i>Sayornis nigricans</i>)	Resident	Feeding young 28 Sept.; nest with eggs found 25 Oct. (CA)		Fraser (1931); E. Walters and WDK, pers. obs.
Say's Phoebe (<i>Sayornis saya</i>)	Variable; resident in southwest	Clutches initiated 4 and 18 Nov. (NV)		Ackerman (1988); Schukman and Wolf (1998)
Blue Jay (<i>Cyanocitta cristata</i>)	Resident	Fledglings on 2 Dec. (AR)	Year of large acorn crop	Marshall (1949)
Western Scrub-Jay (<i>Aphelocoma californica</i>)	Resident	Clutch laid 8 Sept. (CA)		Orians (1960); Stanback (1991)
Pinyon Jay (<i>Gymnorhinus cyanocephalus</i>)	Resident (C)	Egg-laying 16 Aug.–3 Sept. (NM)	Green cones and piñon pine seeds stimulate breeding	Ligon (1971, 1974)
Common Raven (<i>Corvus corax</i>)	Resident	Three records of fall nesting in Great Britain		Mearns and Mearns (1989); Boarman and Heinrich (1999)
Cave Swallow (<i>Petrochelidon fulva</i>)	Some seasonal movement (C)	Nest construction as late as 19 Oct. (NM); some evidence for nests in Oct. and Nov. in Jamaica		Downer and Sutton (1990); West (1995)
Barn Swallow (<i>Hirundo rustica</i>)	Migratory (C)	Older nestlings on 24 Sept. (SASK)		Pettingill (1946)
Bewick's Wren (<i>Thryomanes bewickii</i>)	Mostly resident	Specimen taken 12 Dec. showed unmistakable evidence of breeding (CA)		Abbott (1927)
Sedge Wren (<i>Cistothorus platensis</i>)	Short-distance migrant	Nest with eggs found early Sept. (KS)		Schwilling (1982)
Eastern Bluebird (<i>Sialia sialis</i>)	Partial migrant	Eggs to mid-Sept.; occasional nesting in Sept. and Oct.		Gowaty and Plissner (1998)
California Thrasher (<i>Toxostoma redivivum</i>)	Resident	Several nests recorded in Nov. (CA)	Occurred after mild temperatures followed first winter rains	Sargent (1940); Orians (1960)
Cedar Waxwing (<i>Bombycilla cedrorum</i>)	Some seasonal movement (C)	Active nests in late Sept. and early Oct. (NY; ON; ALB)		Hamilton (1933); Speirs (1985); G. Yaki, pers. comm.

TABLE 2. Continued.

Species	Migratory status (coloniality) ^a	Evidence ^b	Notes	Reference
Yellow Warbler (<i>Dendroica petechia</i>)	Migrant	Clutch collected 17 Nov. (CA)		WFVZ
Olive Sparrow (<i>Arremonops rufivirgatus</i>)	Resident	Nest with eggs found 7 Sept. (TX)		Merrill (1879)
Canyon Towhee (<i>Pipilo fuscus</i>)	Resident	Nest with eggs found 8 Sept. (AZ); nesting occasionally occurs Feb.–Oct.	Bimodal nesting season related to desert rains	Marshall and Johnson (1968); Ohmart (1973); Johnson and Haight (1996)
Abert's Towhee (<i>Pipilo aberti</i>)	Resident	Fresh clutch found 10 Sept. (AZ)	Some Sept.–Oct. males had cloacal protuberances	Bendire (1890)
Rufous-winged Sparrow (<i>Aimophila carpalis</i>)	Resident	Late eggs 1–11 Sept. (AZ); nestlings with unopened eyes 16 Sept. (TX)		Bendire (1882); Smith (1917); Ohmart (1969); Wolf (1977)
Rufous-crowned Sparrow (<i>Aimophila ruficeps</i>)	Resident	Young nestlings 16 Sept. (TX)		Smith (1917)
Field Sparrow (<i>Spizella pusilla</i>)	Partial migrant	Feeding fledglings 10 Oct. (OH)		Walker (1937)
Black-throated Sparrow (<i>Amphispiza bilineata</i>)	Some seasonal movement	Eggs as late as 13 Sept. (AZ)		Banks (1968)
Grasshopper Sparrow (<i>Ammodramus savannarum</i>)	Mostly migratory	Nest with eggs 6 Sept. (IL)		Bellrose (1936)
Northern Cardinal (<i>Cardinalis cardinalis</i>)	Resident	Incubating 19 Oct. (WV); nest with eggs 2 Sept. (KS)	Autumn nests fairly common in West Virginia	Christy (1942); D. LaShelle, pers. comm.
Pyrrhuloxia (<i>Cardinalis sinuatus</i>)	Resident	Eggs 3 Sept. (TX)		Tweit and Thompson (1999)
Indigo Bunting (<i>Passerina cyanea</i>)	Migrant	Young in nest 26 Sept. (ON)		Peck and James (1987)
Varied Bunting (<i>Passerina versicolor</i>)	Mostly migratory	First egg of season as late as 14 Aug. (AZ); apparently lay into early Sept.	Breeding delayed until first significant summer rain	Groschupf and Thompson (1998)
Tricolored Blackbird (<i>Agelaius tricolor</i>)	Mostly resident (C)	Egg-laying between 7 Oct. and 5 Nov. in at least 2 colonies (CA)	Followed Sept. rains; possibly related to local agriculture.	Orians (1960)
Western Meadowlark (<i>Sturnella neglecta</i>)	Mostly resident	Recently fledged young in Dec. (CA)	Itinerant breeder. Possibly related to unusually heavy fall rains	Abbott (1927)

TABLE 2. Continued.

Species	Migratory status (coloniality) ^a	Evidence ^b	Notes	Reference
Boat-tailed Grackle (<i>Quiscalus major</i>)	Resident (C)	Egg-laying in Sept. (FL)	Earlier nests flooded	Selander and Nicholson (1962); Kale (1975); Riddell (1976)
House Finch (<i>Carpodacus mexicanus</i>)	Variable; resident in CA (C)	Incubating eggs 24 Nov. and 29 Dec. (CA)		Smith (1930); Howell and Burns (1955)
Red Crossbill (<i>Loxia curvirostra</i>)	Nomadic	Egg dates in N. America from mid-Dec. to early Sept.	Opportunistically related to food supply (cone crop)	McCabe and McCabe (1933); Adkisson (1996)
White-winged Crossbill (<i>Loxia leucoptera</i>)	Nomadic	Nests every month of the year	Opportunistically related to food supply (cone crop)	Benkman (1992)
Lesser Goldfinch (<i>Carduelis psaltria</i>)	Resident (C)	May nest regularly into Oct. and Nov. (CA)		Abbott (1927); Linsdale (1968)
American Goldfinch (<i>Carduelis tristis</i>)	Variable (C)	Latest eggs 24 Sept. (ON); nest with eggs 9 Sept. (KS); nest with old nestlings 10 Oct. (ON)		Peck and James (1987); D. LaSelle, pers. comm.; G. Yaki, pers. comm.
House Sparrow (<i>Passer domesticus</i>)	Resident (C)	Eggs into Sept.; breeds throughout the year in Britain	Introduced	Orians (1960); Lowther and Cink (2006)

^a C = colonial or semicolonial nesting.

^b ALB = Alberta; AR = Arkansas; AZ = Arizona; CA = California; CO = Colorado; FL = Florida; IL = Illinois; KS = Kansas; KY = Kentucky; MI = Michigan; MT = Montana; NM = New Mexico; NY = New York; NV = Nevada; OH = Ohio; ON = Ontario; SASK = Saskatchewan; TX = Texas; UT = Utah; WA = Washington; WV = West Virginia.

^c WFVZ = Western Foundation of Vertebrate Zoology.

TABLE 3. Distribution of fall nesting among North American terrestrial birds in relation to their migratory status and coloniality in nesting. Total species = 441, of which fall nesting was detected in 69 (16%).

Category	Total species	Fall nesting detected	Percent fall nesting
Migratory status			
Primarily or fully migratory	211	11	5
Intermediate ^a	78	16	21
Primarily resident	152	42	28
Nesting coloniality			
Colonial or semicolonial	64	17	27
Not colonial	377	52	14

^a Includes partial migrants, short-distance migrants, species that exhibit seasonal movements, and species whose migration habits are variable or nomadic. Three species were intermediate overall but known to be resident in the locality where fall nesting was reported; they are included in the "intermediate" category here.

of 30 (43%) passerine families (Appendix). Fall nesting was rare among migrants, but was nonetheless detected in 11 (5%) of such species, including Neotropical migrants such as the Barn Swallow (*Hirundo rustica*), Yellow Warbler (*Dendroica petechia*), and Indigo Bunting (*Passerina cyanea*). Fall nesting was significantly more frequent among resident species and among species that nest colonially or semicolonially than among migrants or solitary-nesting species.

Unfortunately, existing scientific collections provide relatively poor information regarding the extent of fall nesting. For example, although fall nesting is clearly a normal, if irregular, feature of Acorn Woodpecker breeding and has been in the literature nearly a century (Myers 1915), of 225 egg sets examined at major collections throughout the United States as part of an earlier study (Koenig 1986), none was collected after 20 July, the cutoff date for fall nests used here. The lack of any fall nests in this sample is clearly due to the failure of early collectors to look for breeding activity late in the season rather than an absence of fall nesting a century ago (Willard 1913). Indeed, a substantial fraction of breeding biology studies of North American birds focus on the spring, often to the near total exclusion of fieldwork later in the year that might reveal fall nesting events. Until this omission is rectified, the real extent of fall nesting, both within and among these often otherwise well-studied species, will remain unknown.

Also unavailable for the vast majority of species is the general frequency distribution of nests beyond the length of the breeding season. The ecological factors facilitating fall nesting

are usually unknown as well, although clearly different factors can be important. In several species, for example, fall nesting is apparently dependent primarily on an irregularly pulsed food supply—seeds, fruits, rodents, or insects—that is very abundant in some years (Ostfeld and Keesing 2000). Acorn Woodpeckers, in which fall nesting occurs in years of large acorn crops, are a good example of such a species, as are Band-tailed Pigeons (*Patagioenas fasciata*), White-crowned Pigeons (*Patagioenas leucocephala*), Common Ground-Doves (*Columbina passerina*), the two cuckoos, Barn Owls (*Tyto alba*), Western Scrub-Jays, Pinyon Jays, and the two crossbills. Several species in which fall nesting appears to be related to particularly heavy or unpredictable rainfall may also belong in this category, assuming that rainfall correlates with subsequent availability of some key food resource.

For the majority of species it is likely that fall nesting is a long-standing part of breeding phenology unrelated to human activity. Four species are possible exceptions. Fall nesting in the Tricolored Blackbird, an itinerant breeder, was hypothesized by Orians (1960) to be related to the local agriculture that now occupies much of its range, while all cases of fall breeding in Boat-tailed Grackles (*Quiscalus major*) reported by Selander and Nicholson (1962) were in city parks, suggesting the importance of urban horticultural practices to providing the conditions required for fall breeding. Both these species are highly social, prompting Selander and Nicholson (1962) to suggest that fall breeding is more likely to occur in colonial species because they are better adapted to respond to temporarily favorable conditions.

Although our survey revealed numerous exceptions to this hypothesis, it also confirmed that fall nesting is indeed significantly more frequent among colonial- and semicolonial-nesting species than solitary species.

The other two species in which fall nesting has been suggested to be related to anthropogenic factors are Anna's Hummingbirds (*Calypte anna*) and Monk Parakeets (*Myiopsitta monachus*). Witzeman (1984) suggested that fall nesting in Anna's Hummingbirds is related to flowering of exotic plants, which are now widespread throughout its range, while Neidermeyer and Hickey (1977) suggested that late nesting in introduced Monk Parakeets is an ecological holdover from their South American origins. The extent to which these hypotheses are valid remains to be determined.

Although there is no reason to believe that fall breeding in most species is a recent phenomenon, it is entirely possible that global warming may increase the frequency of such late nesting in the future. This is suggested by the previously mentioned spate of fall nesting that occurred in Britain during the fall of 1953, during which time mean November temperatures were 1.8°C above average for the region (Snow 1955). Given that this value is well within or below the increases projected to occur due to global climate change (Intergovernmental Panel on Climate Change 2001), it is reasonable to predict that fall nesting will become more frequent among north temperate birds in the future than our current survey suggests has been the case in the 20th century.

In conclusion, fall nesting is more common among North American terrestrial species than generally realized, and is likely to increase in frequency as global warming takes place. Except in the case of long-distance migrants, among which fall nesting is rare (but not unheard of), workers studying birds in temperate regions should assume that fall nesting is a possibility until study during the late summer and fall demonstrates otherwise.

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APPENDIX. Taxonomic summary of species surveyed and the number within each family for which fall nesting is known to occur. The survey included North American terrestrial species that breed north of the Mexican border.

Order	Family	Species surveyed (<i>n</i>)	Species known to nest in fall (<i>n</i>)
Ciconiiformes	Cathartidae	3	0
Falconiformes	Accipitridae	23	5
	Falconidae	7	2
Galliformes	Cracidae	1	1
	Phasianidae	15	0
	Odontophoridae	6	5
Columbiformes	Columbidae	11	8
Psittaciformes	Psittacidae	4	1
Cuculiformes	Cuculidae	6	3
Strigiformes	Tytonidae	1	1
	Strigidae	18	1
Caprimulgiformes	Caprimulgidae	6	0
Apodiformes	Apodidae	4	0
	Trochilidae	14	3
Trogoniformes	Trogonidae	1	0
Coraciiformes	Alcedinidae	2	0
Piciformes	Picidae	22	2
Passeriformes	Tyrannidae	34	4
	Laniidae	2	0
	Vireonidae	13	0
	Corvidae	17	4
	Alaudidae	2	0
	Hirundinidae	8	2
	Paridae	11	0
	Remizidae	1	0
	Aegithalidae	1	0
	Sittidae	4	0
	Certhiidae	1	0
	Troglodytidae	9	2
	Cinclidae	1	0
	Regulidae	2	0
	Sylviidae	4	0
	Turdidae	14	1
	Timaliidae	1	0
	Mimidae	10	1
	Sturnidae	1	0
	Motacillidae	5	0
	Bombycillidae	2	1
	Ptilonotidae	1	0
	Peucedramidae	1	0
	Parulidae	50	1
	Thraupidae	4	0
	Emberizidae	49	8
	Cardinalidae	10	4
	Icteridae	21	3
	Fringillidae	16	5
	Passeridae	2	1