

# LATE BREEDING-SEASON DEFINITIVE PRE-BASIC MOLT BY MALES, AND LATE BREEDING SEASON BROOD CARE BY FEMALES, IN CENTRAL CALIFORNIA WILSON'S WARBLERS

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## Abstract

**Abstract.** I made late breeding season (after 1 July) observations of a central California population of Wilson's Warbler, *Cardellina pusilla*, over nine breeding seasons. I sighted males in definitive prebasic molt from 4 July in 2007 through 1 September in 1999. Possibly all territorial males molted on their breeding territories, and molt lasted a maximum of 46 days. Following prebasic molt, territorial males engaged in subdued "post molt singing," which lasted 14 days in one male, but usually no more than seven days, and was last heard on 6 September in 1999. I sighted no female in definitive prebasic molt, nor in bright basic plumage, during the study. Of 12 color-banded females sighted after 22 July, I confirmed 11 had been in late breeding season uniparental brood care. Possibly all resident females not engaged in late uniparental brood care vacated their breeding territories earlier, and before resident males. They presumably underwent prebasic molt at later times and locations not known. Remaining late nesting females must have molted much later than resident males, and likely later than early departing resident females, and at unknown locations. I last sighted uniparental brood tending females still in dull alternate plumage on 26 and 29 August respectively, whereas some males had completed prebasic molt by 13 August. Three unique study findings are the occurrence of male post molt singing, a male/female difference in location of prebasic molt, and a likely dichotomy of prebasic molt timing between females leaving their breeding grounds early, and those remaining in uniparental brood care.

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**Key Words :** *Cardellina pusilla*, basic plumage, alternate plumage, molt migration, molting grounds, post molt singing, uniparental brood care

## INTRODUCTION

There exists wide variation in the definitive pre-basic molting regimens of migratory passerines. Members of many migratory passerine species undergo complete definitive pre-basic molt, or at least the molt of flight feathers, on their breeding grounds before flying to wintering sites (Vega Rivera *et al.* 1998, Ryder and Rimmer 2003, Rohwer *et al.* 2005). Members of other species begin pre-basic molt before initiating migration, but complete molting during migration (Flockhart 2010). Members of yet other species undertake “molt-migration,” which can involve a wide range of timing and locations (Rohwer *et al.* 2008, Wiegardt *et al.* 2017a, Pyle *et al.* 2018, Tonra and Reudnik 2018), but often involves recognized “molting grounds” (Steele and McCormick 1995, Tonra and Reudnik 2018). Finally, some passerine species migrate to wintering sites before beginning pre-basic molt (Jenni and Winkler 1994).

Regarding sexual differences in the timing of definitive pre-basic molt, males and females of many passerine species initiate definitive pre-basic molt at about the same time, and require about the same amount of time to complete molt, with differences varying by only by a few days (Vega Rivera *et al.* 1998, Heise and Rimmer 2000, Butler *et al.* 2008, Flockhart 2010). In studies that have found significant sex difference in the mean timing of pre-basic molt, most have found that males usually initiate and complete molt earlier than females (Rimmer 1988, Svensson and Nilsson 1997, Ryder and Rimmer 2003, Borowske *et al.* 2017). However, in Wood Thrushes (*Hylocichla mustelina*), under certain circumstances involving late broods, either females or males can molt earlier, varying with the breeding pair (Gow and Stutchbury 2013). Also, few studies have reported mean migratory passage times, which can reflect timing of definitive pre-basic molt, to be earlier for females than for males (for Ruby-crowned Kinglets [*Regulus calendula*, Swanson *et al.* 1999] and for Macgillivray’s Warblers [*Oporornis tolmiei*, Carlisle *et al.* 2005]). The greatest mean difference in timing of definitive pre-basic molt between the sexes that I found in the literature, based on field observations, was a mean twelve days earlier for male Seaside Sparrows (*Ammodramus maritimus*, Borowske *et al.* 2017).

The majority of studies on definitive pre-basic molting, or timing of autumn migratory passage which can relate to timing of molt, have involved late- or post-breeding-season mist-netting (Yong *et al.* 1998; Ryder and Rimmer 2003; Carlisle *et al.* 2005; Wiegardt *et al.* 2017a, b; Pyle *et al.* 2018; Junda *et al.* 2020). One limitation of such studies is that they may not be able to directly evaluate the molting and behavior of individuals that possibly remain on breeding grounds after the majority of individuals have departed for migration. Thus, possible late nesting and delayed molting in those individuals may not be assessed. Also, contrary to direct observation of a color-banded and sexed study population, migrating sexually monomorphic species can be difficult to sex by rapid, non-invasive means in the autumn. Possibly based on that difficulty, and the fact that in many species timing of molt between sexes is minimal in any case, some mist-netting studies have not distinguished molting data based on sex (Wiegardt *et al.* 2017a, b; Pyle *et al.* 2018).

I here report, based on direct field observations, made over nine breeding seasons at a study site in central inner-coastal California, that definitive pre-basic molt in a population Wilson’s Warblers (*Cardellina pusilla*) occurs on the breeding territories for most, and possibly all, resident males. I also report sighting no female in pre-basic molt, nor any female in bright, post-molt basic plumage, at my study site. A relatively few female Wilson’s Warblers did remain on their breeding territories late into the breeding season in drab alternate plumage, however. Most, and possibly all, of these females sighted late in the breeding season

were, or had been, involved in late-breeding-season uniparental brood care. I conclude that most resident females in my study population underwent pre-basic molt at unknown locations away from their breeding grounds. The timing of pre-basic molt in those early-departing females, relative to the timing of male molt, is not known. A relatively few females did remain on their breeding territories most, at least, involved in late-breeding-season brood care. Those females apparently molted much later than did resident males, as I sighted no female in pre-basic molt, and also sighted some still in alternate plumage, after most males had completed pre-basic molt. Those late-breeding-season females also may have initiated pre-basic molt much later than did resident females that left their breeding territories earlier. The locations of molting in females, both those that vacated breeding territories early and those that remained to tend late broods, are not known.

This study fills some missing gaps in our knowledge of definitive pre-basic molt in migratory passerines, and this information likely could not have been obtained by methodology other than comprehensive, direct field observation, which is not a part of many current studies. This study indicates that there was a split between the molting locations of male and at least most female Wilson’s Warblers in my study population. This study cannot evaluate whether females leaving their breeding territories early molted earlier or later than males that stayed and molted on their territories. However, this study suggests a wide separation in the timing of pre-basic molt between females that departed their breeding grounds earlier, and those that remained on territory and raised uniparental, late-breeding-season broods. Late-nesting females also apparently molted much later than males that molted on their breeding territories. Finally, this study documents post-molt singing in most, and perhaps all, male Wilson’s Warblers at my study site. This behavior previously has not been reported for any passerine. However, I and some other workers previously had observed post-molt singing in another warbler species, the Orange-crowned Warbler (*Leiothlypis celata*). This suggests that post-pre-basic molt singing may occur in other wood-warbler species, and possibly in other passerine families as well.

## Material and METHODS

*Study area* – My study area was approximately 0.18 x 0.26 km in dimension, and covered approximately 4.7 ha of parkland in the Tilden Nature Area, East Bay Regional Park District, Contra Costa County, California. The study area was located in an area of low hills and creek valleys to the east of San Francisco Bay, and was bordered on one side by Wildcat Creek, and on the uphill side by oak/bay woodland. The dryer upland woodland was populated mainly by Coast Live Oak (*Quercus agrifolia*) and California Bay Laurel (*Umbellularia californica*), and the riparian woodland along Wildcat creek was populated mainly by willows (*salix* sp.). Wilson’s Warblers tended to prefer moist areas with at least some riparian habitat for nesting, but moved into dryer oak/bay woodland when population numbers were higher.

*Timing and procedures* – This study part of an investigation of Wilson’s Warbler breeding ecology extending over a greater number of years. I made observations of Wilson’s Warbler late season (after one July) breeding, molting, and plumages for varying numbers of days annually from 1998 through 2009, exclusive of years 2000 and 2006. In four of these years (1999, 2001, 2003, and 2004) I extended observations into September, with my latest observations on 19 September, 1999. For identification of individuals, I captured Wilson’s Warblers (BBL permit 22521) in 32 mm poly mist nets of six or seven m length. I banded captured Wilson’s Warblers with a numbered F & W band on one leg and a unique combination of color bands, usually two, on the other leg. I captured most males in single mist nets, placed in their breeding territories and accompanied by audio playback of recorded male song. I also captured many females in this way. I also captured some males and females in multiple nets placed in areas where individuals were active, often males chasing a nest building or exploring female. I determined sex, usually based on presence of cloacal protuberance or brood patch, for all captures, and age for many captures, based on condition of rectrices and/or presence or absence of molt limits in wing coverts (Pyle 1997). During the nine years of my study, I color-banded 40 females and 85 males.

*Observations of male and female molt and plumage* – I assessed the molt and plumage condition of all male Wilson’s Warblers sighted after 1 July during every observation year. I considered an individual male sighted

in weak, fluttering flight, and/or hopping from twig to twig in vegetation, to be molting flight feathers. I also considered absence of rectrices to suggest possible flight feather molt, although rectrices also can be shed as a means of predator evasion (Møller *et al.* 2006, Awasthy 2010). Indeed, observation of some Wilson’s Warblers having no rectrices prior to 1 July, and before initiation of pre-basic molt, indicated that rectrices were lost for reasons other than molting. Detached contour feathers, often plucked loose by a preening individual, I considered indicative of body feather molt. I also considered the contrast between drab, patchy, alternative plumage body feathers and bright basic plumage feathers to be indicative of continuing pre-basic body-feather molt. All above-mentioned conditions (weak, fluttering flight, shedding of body feathers, etc.) are indicative of what Nolan (1978) calls “noticeable molt,” observable in the field. Although I sighted a male beginning noticeable pre-basic molt as early as 4 July, a few males continued to provision nestlings past mid-July while they remained in alternate plumage, with no apparent molting.

The contrast between males in noticeable molt and males that had completed pre-basic molt was evident, and I used the conditions of strong flight and bright basic plumage as indications that pre-basic molt was complete or near completion. However, males in my study area also sang, usually in subdued volume, for short time periods after completing pre-basic molt (see RESULTS), and all such singing males that I sighted were in bright basic plumage and flew well. I thus considered this “post-molt singing” to be an indicator that pre-basic molt was complete, even when an individual was not sighted.

In 1999 and 2001 I made concentrated efforts to observe molting in five and six color-banded males respectively, occupying territories centrally located in my study area. The purpose of these intensive searches was to learn the possible extent to which pre-basic molt in males might happen on their breeding territories, as observing the extent of molting in the small samples might logically be applied to males in the entire study population.

In addition to the information on males, I recorded the sighting dates, noted the molt and plumage status, and recorded any late-season brood care, of females sighted during the late breeding season, mainly after late July.

*Illustration and tabulation of observations* – I developed a graph to illustrate the timing and intensity of relevant events in the nesting, molting, and plumage cycles of male and female Wilson’s Warblers. I summed the number of observations of respective events over five-day intervals from 1 July through 23 September, the last five-day interval of which included 19 September when I made my latest field observations (in 1999). I additionally developed a table stating the specific dates when I made relevant timing observations, as well as relevant numerical tabulations, such as number of molting males sighted.

## RESULTS

I illustrate the chronology and magnitude of plumage and molting observations in Fig. 1, and state the specific dates or numerical tabulations of relevant observations in Table 1. I conclude that most, and possibly all, of male pre-basic molt occurred on the breeding grounds. I observed males in pre-basic molt multiple times during eight of the nine years of my study, and observed males in bright basic plumage and/or post-molt singing multiple times during six of the nine years (Fig. 1, Table 1). I observed definitive pre-basic molt in a male on its breeding territory as early as 4 July, and I did not observe a male in drab, alternate plumage later than 22 July (Fig. 1, Table 1). Of five males holding territories central to my study area in 1999, for which I searched intently following their last observed brood care activities, I sighted four at least once in pre-basic molt. Of six males for which I similarly searched in 2001, I sighted all six at least once in pre-basic molt.

All observed territorial males initiated pre-basic molt between early and late July, and ceased or greatly reduced (one case) brood care at that time. I observed 12 females retain their alternate plumage into the late (> 20 July) breeding season (Table 1), and found 11 of those females to be brooding eggs and/or nestlings into late July, and/or tending fledglings well into August, usually with no male help. Most of the broods tended by these late-season, predominantly uniparental female nesters contained just two eggs and/or young, while most earlier biparental broods contained four eggs and/or young (Ammon and Gilbert 1999).

All of these observed 11 late-nesting females had been paired with a territorial male, while for the one additional female that I observed after 20 July (on 13, 19, and 21 August, 2004), I had seen no evidence that she had had a territorial social mate. That female, during an early-breeding-season nesting, had tended and fledged, on 1 June, a brood of three young entirely by herself. I also observed her feeding those fledglings by herself on 14 and 21 June. Subsequent time, after brood independence, would have allowed that female to have renested and be tending a brood into the late breeding season, and be tending those fledglings into August. The fact that I observed her foraging alone, and not tending fledglings in mid-August, does not preclude the possibility that she still could have had a late-breeding-season nest which was depredated, however. If that were the case, it is possible that that female also could have initiated a late-breeding-season brood, as did all other brood-tending females I sighted in the late breeding season.

Although I never sighted a female in pre-basic molt, nor in bright basic plumage, during this study, I did confirm some females remaining on my study site in drab, alternate plumage late into August, with the latest sighting being on 29 August (Fig. 1, Table 1). Based on the great difference in respective number of each sex that I sighted in pre-basic molt or basic plumage as opposed to alternate plumage (Table 1, Fig. 1), there was a highly significant difference ( $P < 0.0001$ , Fisher's Exact Test) between the sexes in terms of late-breeding-season plumage and molting.

Post-molt singing was characteristic of territorial males upon completion of pre-basic molt. I indicate the earliest and latest dates, and the maximum number of days for individual males, that I heard post-molt singing (Table 1). The singing appeared to be coordinated with the completion of pre-basic molt, and I considered post-molt singing to be a reliable indicator that that molt was completed. Post-molt singing was similar in pattern to singing I heard earlier in the breeding season, but usually was subdued in amplitude. However, in 2001, a year when there appeared to have been an elevated late-breeding season food supply in my study area, as suggested by, among other things, an unusually high number of mixed-species flocks sighted (WMG, personal observation), the amplitude of post-molt singing in some Wilson's Warbler males sounded similar in amplitude to song heard earlier in the breeding season.

## DISCUSSION

Findings of this study indicate that many, and possibly all, resident male Wilson's Warblers in my study population molted on their breeding grounds. However, since all females I sighted were in drab alternate plumage, with the last sighting being on 29 August (2003), pre-basic molt in females, if it did occur at my study site, likely would have started at least two months later than the first confirmed pre-basic molt in males (4 July, 2007). This seems unlikely. There existed 40 color banded female Wilson's Warblers in my study area during the nine years of my study, which was less than half the number of color-banded territorial males (85). Even so, that number of females was sufficient that, had any of those females been present and in pre-basic molt or bright basic plumage in my study area, I likely would have sighted some.

The most probable conclusions from my study are that most, and possibly all, females at my study site vacated the study site while still in alternate plumage. Given that pre-basic molt in most passerines has been found to occur at similar times for males and females (Vega Rivera *et al.* 1998, Heise and Rimmer 2000, Butler *et al.* 2008, Flockhart 2010), it seems likely that pre-basic molt in most of the females nesting in my study population occurred, not at times greatly different than molting in males, but at sites that were different, and at sites other than their breeding grounds. The exceptions to this possibility related to females that uniparentally tended late-breeding-season broods. These females remained on their breeding territories late into the breeding season and, although I have no information on the timing or location of their presumed pre-basic molt, it no doubt was very late, and likely occurred after their late-season, uniparental broods were independent. This presumed very late molting in the late-breeding, uniparental female Wilson's Warblers that I observed may reflect a facultative, adaptive tradeoff between current reproductive productivity and future fitness (Svensson and Nilsson 1997, Hemborg 1999). This presumed very late molting in some of my females also suggests an extreme timing dichotomy in molting between female Wilson's Warblers that vacate their breeding territories relatively early, and those that remained to raise late-season, uniparental broods.

No other study, to my knowledge, has evaluated the differential timing and location of molting in Wilson’s Warbler sexes. However, some studies have provided information on migratory passage of Wilson’s Warbler sexes, which might indirectly reflect timing of pre-basic molt. Carlisle *et al.* (2005) obtained information on fall migratory passage of passerines at a netting site in southwestern Idaho. While males and females of most species migrated through their netting sites at times not significantly different, for Wilson’s Warblers mean passage of males significantly preceded that of females by five days. However, two other studies of Wilson’s Warbler migratory passage, Otahal (1995), with data from a mist netting operation in central coastal California, and Yong *et al.* (1998), with data from a mist netting operation in riparian habitat along the Rio Grande in New Mexico, found no significant differences in mean autumn migratory passage time of the sexes. Factors which may have contributed to the differences of their results and those of Carlisle *et al.* (2005) are not known, and no firm conclusions can be drawn from those studies regarding Wilson’s Warbler molting, except possibly that mean molting times between the sexes may be similar, and in any case may not differ by more than a week. Also, if there is a difference in mean pre-basic molting times between the sexes within some populations, males may precede females. These conclusions would apply, of course, only to the majority of females in breeding populations, and not to late-breeding and presumably late-molting females as observed in this study. The relative timing, and location, of pre-basic molt in this behavioral subset of females are completely unknown, except that the timing must be very late.

Wiegardt *et al.* (2017b) provided evidence that a proportion of Wilson’s Warblers from their study sites in northern California and southern Oregon traveled upslope following breeding, and underwent pre-basic molt at higher elevations. However, they also found that many individuals remained and molted on their breeding territories over the entire range of their breeding elevations, and thus did not engage in molt migration. Wiegardt *et al.* (2017b) state that their results suggest a variation in strategies for molting and molt migration among Wilson’s Warblers. The study of Wiegardt *et al.* (2017b) was based on analysis of large data sets from mist net captures, and did not separate information for males and females. This study provides a possible explanation for the dichotomy of results obtained by Wiegardt *et al.* (2017b), however. The proportion of Wilson’s Warblers documented as molting on their breeding territories may have been males, while the proportion documented as participating in upslope molt migration may have been females.

I documented post-molt singing occurring in most of the territorial male Wilson’s Warblers that I observed following their pre-basic molt. I know of no previous published reports for post-molt singing behavior in passerines. This does not mean, however, that this behavior has not previously been observed. In 1995 Jim Steele contacted me regarding hearing Orange-crowned Warblers (*Leiothlypis celata*) singing at MAPS netting sites in high-elevation mountain meadows where they do not breed, and in connection with molt migration to these “molting grounds” (Steele and McCormick, 1995). These workers did not report this post-molt singing in their co-authored note. However, I visited a high-elevation netting site with Steele in late June of 1995, confirmed the singing, and made a voice recording of a singing male. Additionally, on 7 August, 2001, during a year with possibly unusually high arthropod food supply into August in my study site, I observed and heard an Orange-crowned Warbler singing weakly on its breeding territory. This was the only male that I ever encountered that late in the breeding season, since Orange-crowned Warblers usually had vacated their breeding territories at my study site by early July (Gilbert *et al.* 2020). Since I have confirmed post-molt singing in two species of wood warbler, it seems quite possible that brief periods of singing following definitive pre-basic molt could be more widespread among wood warblers, and perhaps among passerine species in general, than currently is recognized. Regarding the adaptive function of such singing, it might be presumed that it has a territorial function, with territorial males signaling a warning to other males prospecting for future territories. This function might apply to post-molt singing in male Wilson’s Warblers at my study site. However, the fact that post-molt singing in Orange-crowned Warblers occurred on molting grounds, and based on my observations usually not on breeding grounds, suggests that other adaptive functions must apply for that species.

I conclude with an observation regarding the general approach of this study, compared with approaches of many other recent ornithological studies. Many other studies do not involve “boots on the ground” comprehensive, direct field observation. These studies often are based on more indirect approaches, such as

use of geolocators and small radio transmitters, analyses based on molecular genetics, analyses based on examination of museum specimens, and analyses based on computation of large amounts of data from mist-netting operations. Studies using these approaches contribute greatly to ornithology. Even so, comprehensive direct field observation still likely plays an important role in modern ornithology, and such studies can provide information not obtainable by other means.

Data Accessibility – Cumulative count data for different sexes, molts, and plumage stages for Wilson’s Warblers in the late breeding season are deposited in a Dryad file.

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