*J. Field Ornithol.* 88(1):47–52, 2017 DOI: 10.1111/jofo.12185

# Post-breeding population dynamics indicate upslope molt-migration by Wilson's Warblers

Andrew K. Wiegardt,[1,2,4] Daniel C. Barton,[2] and Jared D. Wolfe[1,3]

[1] *Klamath Bird Observatory, 320 Beach Street, Ashland, Oregon 97520, USA*
[2] *Department of Wildlife, Humboldt State University, 1 Harpst Street, Arcata, California 95251, USA*
[3] *USDA Forest Service, Pacific South West Research Station, Redwood Sciences Lab, 1700 Bayview Drive, Arcata, California 95521, USA*

Received 5 August 2016; accepted 19 December 2016

ABSTRACT. Molt is an energetically costly process, and songbirds (Order Passeriformes) exhibit a diversity of strategies to maximize their survival and reproductive success while meeting the energetic demands of the annual prebasic molt. Nearctic-Neotropic migrants in western North America commonly exhibit one of three strategies: (1) remain in breeding areas to molt, (2) migrate long distances to molt before continuing to wintering areas, or (3) migrate to wintering areas and then molt. Among species that molt in or near breeding areas, the nature of small-scale movements to undergo molt remains largely unknown. We used banding data collected over a period of 27 yr and across an elevational gradient to examine the propensity of Wilson's Warblers (*Cardellina pusilla*) to molt and breed at the same or different locations in northern California and southern Oregon. We found that individual adult Wilson's Warblers were more likely to breed at lower elevations and molt at higher elevations, suggesting that some individuals move altitudinally after breeding to complete the definitive prebasic molt. Such altitudinal movements may be more common among Nearctic-Neotropic migrants in western North America than previously thought.

RESUMEN. **Dynamica poblacional post reproductiva indica migración altitudinal para la muda en *Cardellina pusilla***

La muda es un proceso que es energéticamente costoso y las aves paseriformes muestran una diversidad de estrategias que maximizan la supervivencia y el éxito reproductivo mientras que satisfacen las demandas energéticas requeridas por la muda pre-básica anual. Aves migratorias boreales (Neartico - Neotropico) en el oeste de Norte América, comúnmente tienen tres estrategias: (1) mantenerse en las áreas de reproducción para mudar, (2) migrar largas distancias para mudar antes de continuar hacia áreas donde pasan el invierno, o (3) migrar a áreas de invierno y luego mudar. Entre las especies que mudan en o cerca de áreas de reproducción, la naturaleza de los movimientos a pequeña escala para someterse a la muda sigue siendo en gran medida desconocida. Utilizamos datos de anillamiento colectados a lo largo de un periodo de 27 años y a lo largo de un gradiente de elevación, con el fin de examinar la propensidad de *Cardellina pusilla* de mudar y reproducirse en la misma o en diferentes localidades en el norte de California y sur de Oregon. Encontramos que individuos adultos de *Cardellina pusilla* son más propensos a reproducirse a elevaciones bajas y mudar a elevaciones altas, sugiriendo que algunos individuos se mueven altitudinalmente después de la reproducción para completar su muda pre-básica definitiva. Estos movimientos altitudinales pueden ser más comunes en migrantes boreales (Neartico - Neotropico) en el oeste de Norte América que lo que anteriormente se pensaba.

*Key words:* bird banding, *Cardellina pusilla*, mist net, molt strategy, molt timing, Pacific Northwest

Molt is an underappreciated aspect of avian life history that may interact with survival and reproduction (Hemborg and Lundberg 1998, Dawson et al. 2000). A diversity of molt strategies, including variation in extent, phenology, and timing relative to other life history events such as breeding and migration, have likely evolved in response to seasonal and geographic variation in food availability, climate, and predation risk (Rohwer et al. 2005, Barta et al. 2007). For example, many temperate species apparently have truncated breeding seasons and then molt in their breeding areas while food resources are still plentiful (Gaston 1981); other species migrate longer distances and apparently exploit extensive food resources in monsoonal regions to complete molt (Pyle et al. 2009). Alternatively, some species (e.g., flycatchers in the genus *Contopus*) migrate to wintering areas and then undergo prebasic molt (Pyle et al. 1997). Long-distance molt-migration has been documented in both Nearctic and Palearctic passerines, where birds attempt to maximize food resources during molt by

[4] Corresponding author. Email: andrewwiegardt@yahoo.com

leaving increasingly dry environments and moving to seasonally wet ones (Bensch et al. 1991, Pyle et al. 2009). Available water in temperate environments partly drives primary productivity which, in turn, may increase availability of arthropods for molting birds (Robinson et al. 2013).

In addition to long-distance molt-migration and molt in wintering areas, Rohwer et al. (2008) found that Cassin's Vireos (*Vireo cassinii*) followed a strategy, where individuals leave breeding areas at lower elevations (500 to 800 m) to presumably track food resources at higher elevations (800 to 1200 m) where they undergo molt. Other investigators have also reported small-scale altitudinal movements. In the Sierra Nevada Mountains, Steele and McCormick (1995) captured breeding Orange-crowned Warblers (*Oreothlypis celata*) only at their low-elevation banding station from late March to mid-June. However, after the breeding season, some adults initially captured breeding at the low-elevation site were captured while molting flight feathers at a mid-elevation station from mid-June until September. Butler et al. (2002) found that juvenile Western Tanagers (*Piranga ludoviciana*) moved to nearby montane regions to molt body feathers during the preformative molt before departing on migration.

Several factors might explain post-breeding altitudinal movements by Neotropical-migrant songbirds. These include (1) generally wetter conditions at higher elevations and subsequently more food resources during the molting period (August–October), (2) montane meadows at higher elevations produce an abundance of insects during the molting period, and/or (3) asymmetrical timing in insect phenology between low and high elevations results in more insect food resources at higher elevations during the molting period. Given the evidence that some individuals of at least a few western passerines move upslope to molt, possibly for the aforementioned reasons (Steele and McCormick 1995, Butler et al. 2002, Rohwer et al. 2008), we predicted that other species of western Neotropical migrants would exhibit similar upslope movements.

Thus, our objective was to test the hypothesis that Wilson's Warblers move altitudinally after breeding to molt. If Wilson's Warblers move to higher elevations to molt after breeding, we predicted that a greater proportion of molting birds would be captured at higher elevations relative to lower ones. We also predicted that, compared to high-elevation sites, a greater proportion of Wilson's Warblers captured at lower elevations would be in breeding condition (Ammon and Gilbert 1999). To test these predictions, Wilson's Warblers were captured at a number of sites throughout the Klamath-Siskiyou bioregion of northern California and southern Oregon to examine possible elevational differences in the number of birds either in breeding condition or undergoing molt.

## METHODS

Our study was conducted in the Klamath-Siskiyou bioregion of northern California and southern Oregon. Data were collected from 1982 to 2011 at 17 banding stations. Stations were operated for two to 27 yr (mean = 12.2 yr; Table 1). Each station had eight to 15 12-m mist-net sites spaced at least 20 m apart. One banding station (HOME) was operated year round and others were operated from April until October; we operated each banding station at least once every 10 d during months of operation. Only rarely were some stations not operated during a 10-d period and, across all years, effort was similar from May to October. We opened nets 15 min before sunrise and operated nets for 5 h during each day of sampling, weather permitting. For each captured Wilson's Warbler, we determined age by examining the degree of skull ossification, feather wear of the outermost four primaries, feather shape of the tail and primary coverts, and the presence of a molt limit (Pyle et al. 1997). We considered birds older than their first calendar year to be adults.

We assessed breeding and molt condition of captured adult Wilson's Warblers for individuals that were captured and then recaptured (for a minimum of two captures) at each banding station. By limiting our analysis to recaptured birds, we minimized biases caused by the presence and absence of nonterritorial individuals or erroneous data collected during a single capture. We only included birds from stations where more than five Wilson's Warblers were captured. We considered birds to be breeding by the

Table 1. Latitude and longitude (WGS84) and elevations of 17 banding stations in southern Oregon and northern California, with the total number of adult Wilson's Warblers ($N = 360$) recaptured at the same banding station more than 7 d after initial capture.

| Station | Latitude | Longitude | Elevation (m) | *N* | Years operated |
|---|---|---|---|---|---|
| MAST | N 39.74° | W −122.84° | 1847 | 14 | 7 |
| PLME | N 39.73° | W −122.85° | 1846 | 11 | 6 |
| ANT1 | N 41.49° | W −121.94° | 1656 | 74 | 18 |
| JOHN | N 42.25° | W −122.23° | 1559 | 20 | 15 |
| 7MIL | N 42.71° | W −122.07° | 1279 | 7 | 16 |
| GROV | N 40.96° | W −123.48° | 1258 | 10 | 16 |
| INVA | N 40.52° | W −123.35° | 1187 | 16 | 16 |
| SKSW | N 42.46° | W −122.40° | 1096 | 19 | 7 |
| YACR | N 40.56° | W −124.06° | 49 | 18 | 10 |
| LOST | N 41.33° | W −124.02° | 42 | 23 | 3 |
| MARI | N 40.85° | W −123.99° | 33 | 31 | 13 |
| LELA | N 40.54° | W −124.14° | 16 | 13 | 10 |
| WREF | N 40.78° | W −124.12° | 16 | 57 | 16 |
| RECR | N 41.30° | W −124.04° | 11 | 18 | 8 |
| NAVR | N 39.20° | W −123.75° | 6 | 10 | 2 |
| HOME | N 40.89° | W −124.14° | 6 | 12 | 27 |
| PARK | N 40.89° | W −124.14° | 6 | 7 | 17 |

presence of either a vascularized or wrinkled brood patch or a medium or large cloacal protuberance (Ralph et al. 1993), and categorized molting birds by the presence of symmetrical flight feather molt, indicative of the adult post-breeding molt or definitive prebasic molt (sensu Wolfe et al. 2014). We also noted if any breeding Wilson's Warblers were recaptured at multiple sites. For each Wilson's Warbler, we determined if the individual was ever captured showing evidence of breeding or molting, thus not biasing our results by including multiple samples from any one bird.

We used two separate mixed-effect logistic regression models to test whether the probability of molting and breeding were predicted by changes in elevation. The binomial response was molting (1) and not molting (0) for the first model, and breeding (1) and not breeding (0) for the second model, with a random-intercept effect of station and elevation (km) of the banding station as the fixed explanatory variable. We used program R (R Development Core Team 2014) to conduct logistic regression. We calculated an odds ratio and its confidence interval by raising *e* to the power of the beta estimates from each logistic regression. We tested the sensitivity of the model's predictions to the two most data-rich stations by removing them and rerunning the models. The stations removed were at the extremes of the elevational gradient of our study area, including ANT1, a high-elevation station (1656 m; $N = 74$ individuals), and WREF, a low-elevation station (16 m; $N = 56$ individuals).

## RESULTS

From 1982 to 2011, we captured 9701 Wilson's Warblers, including 1019 captures of 360 adults captured more than once at 17 stations at different elevations. No individuals moved between banding stations. Elevation (km) predicted both the probability of captured Wilson's Warblers displaying molt (mixed-effect logistic regression, $\beta = 0.907$, SE = 0.352, $P = 0.01$) and the probability of captured birds displaying breeding characteristics (mixed-effect logistic regression, $\beta = -1.369$, SE = 0.598, $P = 0.022$). We calculated odds ratios to estimate the magnitude of the effect of elevation on the probability of Wilson's Warblers molting and breeding. For every 1000-m increase in elevation, recaptured Wilson's Warblers were 2.47 (95% CI = 1.24–4.94) times more likely to display molt (Fig. 1). The opposite was true for breeding, Wilson's Warblers were 3.93 (95%

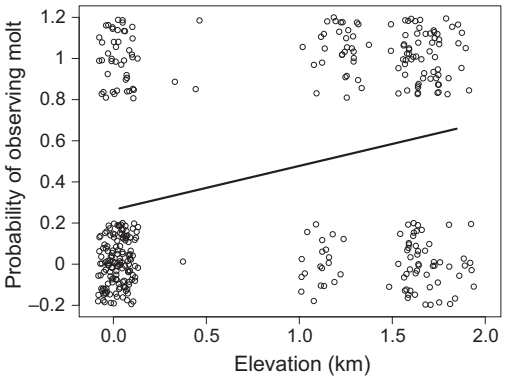


Fig. 1. Logistic regression line showing the effect of elevation on the probability of molting for Wilson's Warblers ($N = 360$) captured at constant-effort mist-netting stations in northern California and southern Oregon. Data points were spread with a jitter function horizontally and vertically to ease visualization.

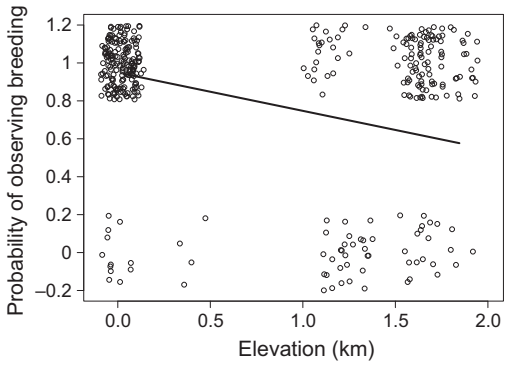


Fig. 2. Logistic regression line showing the effect of elevation on the probability of breeding for Wilson's Warblers ($N = 360$) captured at constant-effort mist-netting stations in northern California and southern Oregon. Data points were spread with a jitter function horizontally and vertically to ease visualization.

CI = 1.22–12.70) times more likely to be in breeding condition with every 1000-m decrease in elevation (Fig. 2).

To examine the sensitivity of our results to the most data-rich stations, we removed the Wilson's Warblers captured at the ANT1 and WREF banding stations and used the pruned dataset in the same mixed-effect logistic regression models. Models showed the same qualitative results for molting (logistic regression, $\beta = 0.930$, SE = 0.396, $P = 0.019$) and breeding (logistic regression, $\beta = -1.106$, SE = 0.562, $P = 0.049$), indicating that predictions from the original models were not sensitive to the two most data-rich banding stations. The three stations (7MIL, GROV, and INVA; Table 1) with the largest proportions of molting, but not breeding, birds were high-elevation banding stations (1187–1279 m; Fig. 3).

## DISCUSSION

Our results suggest that Wilson's Warblers in the Klamath-Siskiyou bioregion were more likely to be in breeding condition at lower elevations, and more likely to be molting at high-elevation stations later in the year. Although no individuals were detected moving from lower- to high-elevation stations, our results support the hypothesis that some Wilson's Warblers undergo an altitudinal molt-migration. Another possible explanation for our results is that birds captured molting at our high-elevation sites did not breed that year and remained there to molt, but this seems unlikely for a relatively short-lived Neotropical migrant songbird. Alternatively, birds that breed further north at similar high elevations may have molted following movement to high-elevation areas in the Klamath-Siskiyou Bioregion, which would represent latitudinal, rather than altitudinal, molt-migration.

Apparent altitudinal movements between breeding and molting areas suggest that Wilson's Warblers may structure energetically taxing phases of their life cycle around shifting food resources along an altitudinal gradient (Rohwer et al. 2008). In support of this hypothesis, R. Burnett (pers. comm.) captured several species of insectivorous warblers, such as Yellow-rumped Warblers (*Setophaga coronata*) and Orange-crowned Warblers, in large numbers (over 35% of total annual captures) during the post-breeding period at high-elevation meadows in the Sierra Nevada Mountains where they do not breed. In addition, capture rates were 225% higher in dry years and the young-to-adult ratio was 82% higher. Such results, in combination with those reported in previous studies (Steele and McCormick 1995, Butler et al. 2002, Rohwer et al. 2008), suggest that some western songbirds are more likely to move upslope to

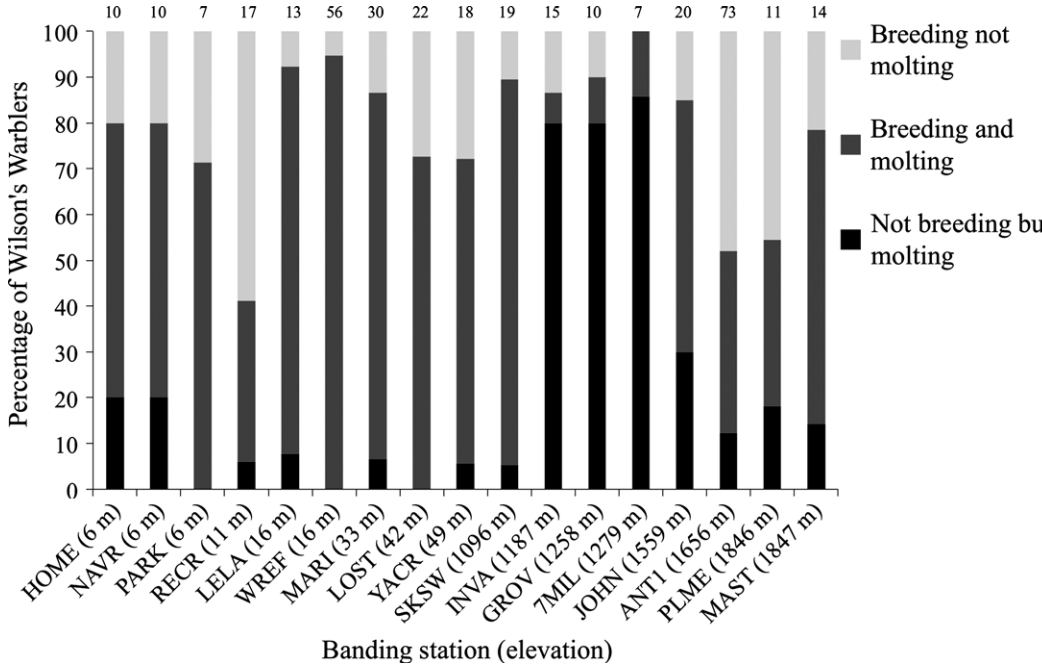


Fig. 3. Stacked bar plot showing percentage of Wilson's Warblers where we obtained evidence of breeding and molting, breeding, but not molting, and molting, but not breeding at each banding station with 10 or more birds also recaptured at the station. Numbers above bars indicate sample sizes and, along the *x*-axis, elevations of each station are provided in parentheses.

presumably more productive habitats during dry years in western forests. Montane meadows at higher elevations may serve as moisture refugia later in the season, providing more food resources for post-breeding Wilson's Warblers and other species of songbirds that are undergoing molt (Holmgren and Hedenström 1995, Rohwer et al. 2008).

Patton and Judd (1970) estimated that wet meadows were more than nine times more productive than forested habitats in New Mexico and Arizona. Because most wet mountain meadows are maintained by streams or sub-irrigated by springs, they often have more foliage and remain more productive when surrounding habitats have dried out (Beck and Peek 2004). When there are fewer wet areas at lower elevations, some insectivorous species may congregate in habitats that produce insects late in the season, such as montane meadows. These processes may explain the upslope movements of some Wilson's Warblers to undergo molt before migrating.

These upslope movements may have gone largely undetected due to the dynamic and complex structure of food resources and topography throughout northern California and southern Oregon. Our results also suggest variation in strategies among Wilson's Warblers in this region, with some individuals molting and breeding at the same site across the entire range of elevations we examined. However, we still found that more captured Wilson's Warblers were molting at high elevations and breeding at lower elevations. The mechanisms that determine the proximate expression of such variation in a population may be informative about the evolution of this particular strategy. Examining altitudinal migration and use of montane meadows during molt by other western bird species is an important step toward recognizing the ecological and conservation value of high-elevation habitats during the post-breeding season. Although we suggest that elevational variation in seasonal productivity of food resources causes upslope movements to molt, other explanations such as predation risk, climate, and availability of water may also be contributing factors.

**ACKNOWLEDGMENTS**

This project was made possible through the vision and dedication of J. Alexander, C. J. Ralph, B. Frey, and J. Stephens. Without their contributions and continuing support of long-term bird monitoring, data used in our analysis would never have been made available. We thank C. Morrison, S. Rohwer, G. Ritchison, and an anonymous reviewer for their help reviewing this manuscript. We also thank the numerous other people from Klamath Bird Observatory, Humboldt Bay Bird Observatory, and Redwood Sciences Lab who contributed to this dataset.

## LITERATURE CITED

AMMON, E. M., AND W. M. GILBERT. 1999. Wilson's Warbler (*Wilsonia pusilla*). In: The Birds of North America (F. Gill and A. Poole, eds.). Academy of Natural Sciences, Philadelphia, PA, and American Ornithologists' Union, Washington, D.C.

BARTA, Z., J. M. MCNAMARA, A. I. HOUSTON, T. P. WEBER, A. HEDENSTRÖM, AND O. FERO. 2007. Optimal moult strategies in migratory birds. Philosophical Transactions of the Royal Society B 363: 211–229.

BECK, J. L., AND J. M. PEEK. 2004. Herbage productivity and ungulate use of northeastern Nevada mountain meadows. Rangeland Ecology & Management 57: 376–383.

BENSCH, S., D. HASSELQUIST, A. HEDENSTRÖM, AND J. M. OTTOSSON. 1991. Rapid moult among Palearctic passerines in West Africa- an adaptation to the oncoming dry season? Ibis 133: 47–52.

BUTLER, L. K., M. G. DONAHUE, S. ROHWER, AND F. MOORE. 2002. Molt-migration in Western Tanagers (*Piranga ludoviciana*): age effects, aerodynamics, and conservation implications. Auk 119: 1010–1023.

DAWSON, A., S. A. HINSLEY, P. N. FERNS, R. C. BONSER, AND L. ECCLESTON. 2000. Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. Proceedings of the Royal Society B 267: 2093–2098.

GASTON, A. J. 1981. Seasonal breeding, molting and weight change among birds of dry deciduous forest in North India. Journal of the Zoological Society of London 194: 219–243.

HEMBORG, C., AND A. LUNDBERG. 1998. Costs of overlapping reproduction and moult in passerine birds: an experiment with the Pied Flycatcher. Behavioral Ecology and Sociobiology 43: 19–23.

HOLMGREN, N., AND A. HEDENSTRÖM. 1995. The scheduling of molt in migratory birds. Evolutionary Ecology 9: 354–368.

PATTON, D. R., AND B. I. JUDD. 1970. The role of wet meadows as wildlife habitat in the Southwest. Journal of Range Management 23: 272–275.

PYLE, P., S. N. HOWELL, D. F. DESANTE, AND R. P. YUNICK. 1997. Identification guide to North American birds. Slate Creek Press, Bolinas, CA.

———, W. A. LEITNER, L. LOZANO-ANGULO, F. AVILEZ-TERAN, H. SWANSON, E. G. LIMÓN, AND M. K. CHAMBERS. 2009. Temporal, spatial, and annual variation in the occurrence of molt-migrant passerines in the Mexican monsoon region. Condor 111: 583–590.

R DEVELOPMENT CORE TEAM. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RALPH, C. J., G. R. GEUPEL, P. PYLE, T. E. MARTIN, AND D. F. DESANTE. 1993. Handbook of field methods for monitoring landbirds. USDA Forest Service General Technical Report PSW-GTR-144, Pacific Southwest Research Station, Forest Service, U. S. Department of Agriculture, Albany, CA.

ROBINSON, T. M., K. J. LA PIERRE, M. A. VADEBONCOEUR, K. M. BYRNE, M. L. THOMEY, AND S. E. COLBY. 2013. Seasonal, not annual precipitation drives community productivity across ecosystems. Oikos 122: 727–738.

ROHWER, S., L. K. BUTLER, D. R. FROEHLICH, R. GREENBERG, AND P. P. MARRA. 2005. Ecology and demography of east–west differences in molt scheduling of Neotropical migrant passerines. In: Birds of two worlds: the ecology and evolution of migration (R. Greenberg and P. P. Marra, eds.), pp. 87–105. Johns Hopkins University Press, Baltimore, MD.

ROHWER, V. G., S. ROHWER, AND J. H. BARRY. 2008. Molt scheduling of western Neotropical migrants and up-slope movement of Cassin's Vireo. Condor 110: 365–370.

STEELE, J., AND J. MCCORMICK. 1995. Partitioning of the summer grounds by Orange-crowned Warblers into a breeding grounds, adult molting grounds, and juvenile staging areas. North American Bird Bander 20: 152.

WOLFE, J. D., E. I. JOHNSON, AND R. S. TERRILL. 2014. Searching for consensus in molt terminology 11 years after Howell et al'.s "first basic problem." Auk 131: 371–377.