

Incidence of eccentric molt in first-year Wrentits increases with fledge date

Megan L. Elrod, Nathaniel E. Seavy, Renée L. Cormier¹, and Thomas Gardali

PRBO Conservation Science, 3820 Cypress Drive #11, Petaluma, California 94954, USA

Received 5 October 2010; accepted 20 May 2011

ABSTRACT. In some passerines, the extent of preformative molt varies among individuals. Wrentits (*Chamaea fasciata*) undergo either a complete preformative molt or an eccentric (i.e., incomplete) preformative molt where some juvenile remiges are retained through the first cycle. Factors that influence the incidence and extent of molt are largely unknown. Using a 10-yr data set from the Palomarin Field Station in central coastal California, we quantified the incidence of eccentric molt and the degree to which variation in the incidence was associated with fledging date and weather. From 1999 to 2009, 159 Wrentits were banded as nestlings and subsequently recaptured. Of these, 21% of first-year Wrentits underwent eccentric molt. We used logistic regression and an information theoretic approach to compare models with fledging date, weather (annual precipitation and breeding-season temperature), and a random effect of year as predictors of the incidence of eccentric molt. Our top model included a random intercept term for year and a fixed effect for the effect of fledging date; birds that fledged later in the season were more likely to undergo eccentric molt. Although the proportion of individuals that underwent eccentric molt varied among years, models with breeding-season temperature and annual rainfall showed little to no support. Our results suggest that the incidence of eccentric molt is more strongly associated with fledging date than with annual variation in weather. The absence of a correlation with weather suggests that weather does not impose an energetic constraint on molt or, if it does, that birds are constrained in their ability to respond to changes in weather by adjusting the extent of their preformative molt. Other factors, such as nestling condition, may provide alternative explanations for year-to-year variability in the incidence of eccentric molt.

RESUMEN. **Incidente de muda excéntrica en *Chamaea fasciata* durante el primer año incrementa con fecha de abandono del nido**

En algunos paserinos, la cantidad de muda después de la etapa juvenil varía entre individuos. *C. fasciata* sufre una muda después de la etapa juvenil completa o una muda excéntrica (i.e., incompleta) en donde las rectrices de algunos juveniles son retenidas a lo largo del primer ciclo. Los factores que influyen y extienden la muda son en su mayoría desconocidos. Usando una base de datos de 10 años de la estación de campo Palomarin en la costa central de California, cuantificamos la incidencia de la muda excéntrica y el grado en el cual la variación en la incidencia estaba asociada con el día de abandono del nido y el clima. Desde 1999 hasta 2009, 159 polluelos de *C. fasciata* fueron anillados y subsecuentemente recapturados. De estos, el 21% de las recapturas de *C. fasciata* del primer año sufrieron una muda excéntrica. Usamos una regresión logística y una aproximación con información teórica para comparar modelos con fechas de abandono del nido, clima (precipitación anual y temperatura durante la temporada reproductiva), y año como efecto aleatorio para vaticinar la incidencia de la muda excéntrica. Nuestro modelo incluyó un término de intercepto aleatorio para año y un efecto fijo para el efecto de la fecha de abandono del nido; las aves que abandonaron el nido tarde en la temporada aumentaron la probabilidad de experimentar muda excéntrica. Aunque la proporción de individuos que experimentaron muda excéntrica varío entre años, modelos con temperatura durante la temporada reproductiva y precipitación anual mostraron poco o ningún soporte. Nuestros resultados sugieren que la incidencia de la muda excéntrica está más fuertemente asociada con la fecha de abandono del nido que con la variación climática anual. La falta de correlación con el clima sugiere que el clima no impone una restricción energética en la muda o, si lo hace, estas aves están limitadas en sus habilidades de responder a cambios en el clima a través del ajuste en la extensión de su muda después de la etapa juvenil. Otros factores, como la condición de los polluelos, pueden brindar explicación alternativas para la variación año tras año en la incidencia de la muda excéntrica.

Key words: *Chamaea fasciata*, eccentric molt, fledge date, molt, Palomarin, preformative molt, Wrentit

Most birds molt at least once annually to replace feathers that have become worn and faded (Jenni and Winkler 1994, Howell 2010).

In their first year, all passerines undergo a preformative molt where some or all feathers are replaced (Howell 2010). The preformative molt can include body feathers only (partial molt) or can include some (incomplete molt) or all (complete molt) remiges (Pyle 1997a).

¹Corresponding author. E-mail: rcormier@prbo.org

The extent of the preformative molt is generally more extensive for birds at lower latitudes and in more exposed habitats (Howell 2010).

Eccentric molt is a pattern of incomplete wing molt where some inner primaries and outer secondaries are retained while the remainder of the primaries and secondaries are replaced. In this pattern, feathers that are most protected and wear at a slower rate are retained (Howell 2010). Eccentric molt has been documented among a wide range of species in North America (18 of 31 families), but none that are resident of temperate forest habitats. In general, birds exposed to more sun, harsher vegetation (e.g., scrubby habitats), or with longer migrations may be more likely to undergo eccentric molt (Pyle 1998, Pyle et al. 2004, Howell 2010). Among 288 species of North American passerines, Pyle (1997b) found that first-year individuals from 46 (16%) species underwent eccentric molt either during their preformative or prealternate molt.

Within a species, some individuals may undergo complete molt whereas others molt eccentrically, and this proportion can vary among species. Although the ecological factors that influence the extent of molt have been largely untested (Neto and Gosler 2006), several studies have revealed that late-fledged individuals molt fewer feathers (Mulvihill and Winstead 1997, Bojarinova et al. 1999). Determining the proximate factors that influence the extent of molt may allow researchers to predict the ability of birds to respond to changes in such variables.

Wrentits (*Chamaea fasciata*), a nonmigratory species in the family Sylviidae, occur in dense coastal scrub, chaparral, and forested habitats with sufficient understory in western North America (Geupel and Ballard 2002). Wrentits usually have a complete preformative molt (Pyle 1997a). However, Flannery and Gardali (2000) documented the occurrence of eccentric molt in first-year Wrentits, with nine of 16 (56%) first-year Wrentits examined retaining some juvenile flight feathers, typically 1 to 3 outer secondaries and occasionally 1 or 2 inner primaries. In some cases, molt was asymmetrical, with secondary feathers retained on one wing, but not the other (Flannery and Gardali 2000).

Fledging date has been hypothesized to determine whether or not an individual has a complete or eccentric molt (Jenni and Winkler 1994, Flannery and Gardali 2000). If the timing

of molt is triggered by changes in photoperiod or limited by the onset of the energetically demanding conditions of colder weather, reduced food supply, or other constraints, then individuals fledging later in the breeding season may be more likely to exhibit eccentric molt than those that fledge earlier. In addition, local weather conditions might influence molt strategies, i.e., whether or not individuals undergo a complete or incomplete molt (Jenni and Winkler 1994, Mulvihill and Winstead 1997, Butler et al. 2008). To identify factors that predict the incidence of eccentric molt in first-year Wrentits, we used 10 yr of data from the Palomarin Field Station where Wrentits were banded as nestlings and subsequently recaptured.

METHODS

Study site. The Palomarin Field Station is located within the Point Reyes National Seashore in central coastal California (37°55'46.64"N, 122°44'07.68"W). The study area consists of 36 ha of dense coastal scrub. The climate of the study area is Mediterranean, with mild temperatures, dry summers, wet winters, and periods of coastal fog. Precipitation is concentrated during the winter, typically from November to March (Chase et al. 2005). For a detailed description of the study site, see Silkey et al. (1999) and Chase (2002).

Nest monitoring. Wrentit nests were found and monitored by three or four biologists per year from March to August 1999 to 2009 using standardized methods described by Martin and Geupel (1993). Nests were checked at least every 4 d and nestling age determined by either direct observation (Jongsomjit et al. 2007) or calculated from the time of clutch completion and the known incubation period. At 10 d posthatching, or as close to that age as possible, each nestling was fitted with an aluminum USGS band and three plastic color bands as part of a larger demographic study. Banding date was used as a proxy for fledge date because fledging occurs approximately 5 d after banding for all individuals. Fledge date was recorded as the number of days since 1 January. Over the 10 yr of the study, annual mean fledge date (banding date) ranged from 26 May to 9 June. This variability was likely associated with a number of factors, including annual variation in nest survival and the incidence of

double-brooding (Geupel and DeSante 1990). In some systems, mean fledge date correlates with rainfall (Preston and Rotenberry 2006), but the correlation between annual bioyear rainfall and annual mean fledge date of Wrentits is not statistically significant at our study site (PRBO, unpubl. data). On average, approximately 20% of Wrentit pairs at our study site double brood (Geupel and DeSante 1990). However, because we could not identify all nests as first or second broods, we were not able to include this in our analysis.

Constant-effort mist-netting. Ballard et al. (2004) provided a detailed description of the operation of the two adjacent mist net arrays at Palomarin. The daily array (20 nets at 14 sites, 6 sites had 2 nets stacked vertically) was operated 6 d per week (May–November) or 3 d per week (December–April), and the weekly array (10 single nets) was operated once every 10 d, occasionally twice in 10 d. Nets were opened 15 min after local sunrise and kept open for 6 h at both sites, weather permitting. When postfledging Wrentits were captured, we recorded their molt status, including the flight feathers that were actively molting and those that were new and retained.

Defining individuals with eccentric molt. We used the molt terminology proposed by Howell et al. (2003). Wrentits have the complex basic molt strategy, molting only once each year during the late summer through fall (Geupel and Ballard 2002, Howell 2010). First-year birds undergo a preformative molt from about July to October, and the (definitive) prebasic molt usually begins the following year in July or August. Thus, we considered young Wrentits to have eccentric molt if captured between November of their first year and the following July and showing evidence of two generations of flight feathers (from the juvenile and formative plumages). Alternatively, if in a late stage of active molt, eccentric molt could be identified if a bird had not followed the typical complete molt sequence (i.e., if primary molt began with a primary other than the innermost) and had retained a section of remiges. Eccentric molt is occasionally asymmetrical (Jenni and Winkler 1994, Flannery and Gardali 2000), and we considered molt eccentric if the pattern was observed on at least one wing.

Weather data. Daily cumulative rainfall and high and low temperatures have been

recorded at the field station since 1969. We used these data to calculate two metrics: bioyear rainfall and average daily high temperature during the breeding season. Bioyear rainfall measures the total rainfall during the 12-mo period (July–June) preceding the breeding season. This metric combines the months (October–April) when 94% of the precipitation in the region occurs (Chase et al. 2005). In previous studies, bioyear rainfall at Palomarin has been shown to be an important predictor of the number of nesting attempts during a breeding season, the seasonal fecundity (Chase et al. 2005) and annual survival of adult Song Sparrows (*Melospiza melodia*; Dybala, pers. comm.), and the overall number of young birds captured (DeSante and Geupel 1987). Additionally, Preston and Rotenberry (2006) found that during a drought, even Wrentits provided with supplemental food delayed nesting, initiated fewer nesting attempts, fledged young earlier, and had shorter breeding seasons. Thus, we hypothesized that an increase in bioyear rainfall would increase food availability, releasing birds from energetic constraints that may be associated with the proportion of birds with eccentric molt.

We also calculated average daily high temperature for the breeding season (March–September). This metric (hereafter, breeding-season temperature) captures variability associated with weather conditions during the nesting period. Breeding-season temperature may influence several components of passerine reproductive success (Rotenberry and Wiens 1991, Wilson and Arcese 2003, Chase et al. 2005), and we hypothesized that it could either increase the incidence of eccentric molt if arthropod prey are less abundant in hot, dry years, or decrease the incidence if fledglings are released from energetic constraints of thermoregulation during warmer years.

Statistical analysis. We used logistic regression to describe the association between predictor variables and molt type (eccentric or complete). We included year as a random effect in the model using a generalized linear mixed model (Bolker et al. 2009, Zuur et al. 2009). Because few individuals in our analysis came from the same nest, we did not include nest identity as an additional random effect. Models were fitted using the lme4 package (Bates and Maechler 2009) in R version 2.10.0 (R Development Core Team 2009).

Using an information theoretic approach and AICc values (Burnham and Anderson 2002), we compared seven competing models to evaluate biological hypotheses explaining temporal variation in the proportion of individuals that underwent eccentric molt. The full model included random intercept for year, bioyear precipitation, breeding-season temperature, and fledging date as fixed effects. We compared this model to a weather-only model (both weather variables), a rainfall-only model, a temperature-only model, and a fledging date-only model (all with year as a random effect). We also included a model with only year as a random effect. For this set of models, we report the difference in AICc scores between the best supported model and other models, the model likelihood, and the model weight (w_i ; Burnham and Anderson 2002).

RESULTS

Of 1210 nestlings banded from 1999 to 2009, 369 were recaptured at least once. Of 159 captured between November and July of their first year, 33 (21%) exhibited eccentric molt.

Of the seven models, the one that included a random intercept term for year and a fixed effect for the effect of fledging date was better supported than alternative models (Table 1). From this model, we used the estimates of the fixed effects for the intercept ($a = -8.35$) and the slope associated with fledging date ($b = 0.04$) to calculate the fitted values describing the probability of eccentric molt as a function of fledging date. For birds that fledged early in the season, the probability of eccentric molt was < 0.02 , but this probability increased as the season progressed (Fig. 1). For individuals that fledged at the end of the breeding season, the predicted probability of eccentric molt was 0.42.

The random effect model was better supported than a model without random effects, suggesting year-to-year variation in the incidence of eccentric molt. Conditional estimates of the random effects for each year suggest that the incidence of eccentric molt was similar in most years, but that there was a greater incidence of eccentric molt in 2000, 2002, and 2009 (Fig. 2).

DISCUSSION

We found that Wrentits that fledged later in the season were more likely to undergo eccentric

Table 1. Results from an information-theoretic analysis of the incidence of eccentric molt in first-year Wrentits in central coastal California, 1999–2009. Models were ranked using the differences in Akaike's information criterion (ΔAIC_c) corrected for sample size ($N = 159$), Akaike model likelihood, and Akaike model weights (w_i).

Model parameters	ΔAIC_c	Model likelihood	w_i
Fledging date + year (random effect)	0	1	0.87
Fledging date + bioyear rain + breeding season temperature + year (random effect)	3.9	0.15	0.13
Fledging date	9.8	0.01	0.01
Year (random effect)	14.7	<0.01	<0.01
Breeding season temperature + year (random effect)	16.2	<0.01	<0.01
Bioyear rain + year (random effect)	16.6	<0.01	<0.01
Bioyear rain + breeding season temperature + year (random effect)	18.6	<0.01	<0.01

molt. Few investigators have examined the association between fledge date and extent of preformative molt. Michener and Michener (1940) found that the postjuvinal (preformative) molt of House Finches (*Carpodacus mexicanus*) was less extensive for young hatched later in the breeding season, and similar results have been reported for Northern Mockingbirds (*Mimus polyglottos*; Michener 1953) and Savi's Warblers (*Locustella luscinioides*; Neto and Gosler 2006). Additionally, young in second broods of Great Tits (*Parus major*) replaced fewer reproductives and greater coverts than those in first broods that fledged earlier in the nesting season (Bojarinova et al. 1999). Thus, our results support a general pattern for less extensive preformative molt in young that fledged later in the breeding season.

The proximate mechanism responsible for this pattern remains poorly understood. Because photoperiod plays an important role

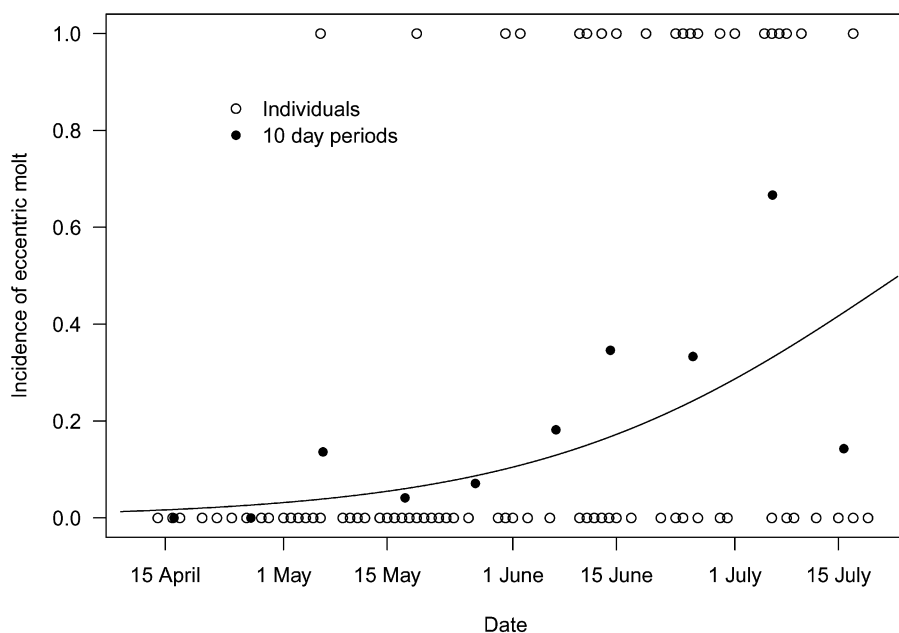


Fig. 1. Occurrence of eccentric molt in first-year Wrentits as a function of fledging date in central coastal California, 1999–2009 ($N = 159$). The line represents the fitted model (fixed effects only) and the dark circles represent the proportions of individuals (all years combined) pooled across 10-d periods across the range of fledging dates.

in regulating hormonal signals that initiate and terminate molt (Dawson 1998, Bojarinova et al. 1999), the association between the extent of molt and fledge date may simply reflect the photoperiods experienced by late-fledging birds. However, if molt were exclusively controlled by photoperiod, we would expect that, after removing the effect of fledging date, there would be little residual variation across years.

Other investigators have documented correlations between weather conditions and the extent or duration of molt by adult birds. For example, Butler et al. (2008) found that Black-capped (*Vireo atricapilla*) and White-eyed (*V. griseus*) vireos molted later in a wet La Niña year than a dry El Niño year, and Howell and Corben (2000) found suspended or protracted wing molt in Black-legged Kittiwakes (*Rissa tridactyla*) and suggested that low food availability resulting from stormy El Niño weather affected feather molt. We found little evidence that either bioyear precipitation or breeding-season temperature were correlated with the proportion of hatch-year birds exhibiting eccentric molt. Although other weather variables, such as timing

of rain (e.g., early versus late winter), might better explain incidence of eccentric molt in Wrentits, we feel that, given the importance of bioyear precipitation and breeding season temperature for Song Sparrow reproductive success and survival (Chase et al. 2005, K. Dybala, pers. comm.), these variables should have captured biologically relevant information about energetic requirements and food availability.

The stronger support for the model including year as a random effect suggests that the incidence of eccentric molt varies among years even after controlling for fledging date. In the absence of an effect of bioyear rainfall and breeding season temperature, there may be several alternative explanations for this variation. One possible explanation is that nestling condition, unrelated to weather (e.g., parasite load), is an important proximate explanation for both annual and individual variation in the occurrence of eccentric molt. However, Bojarinova et al. (1999) found that variation in the condition of nestling Great Tits did not affect the extent of molt and that the extent of molt was reduced for later-fledged birds, suggesting that

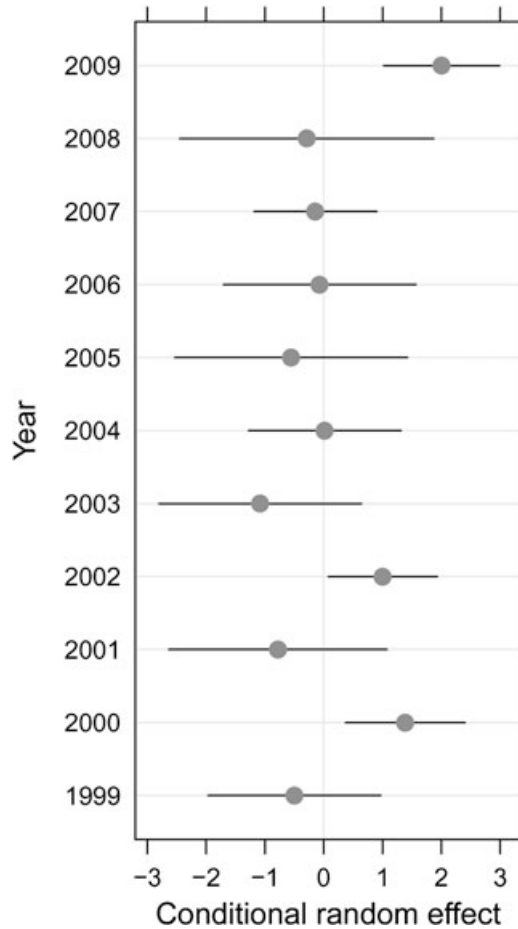


Fig. 2. Conditional random effects (and 95% confidence intervals) describing annual variation in the occurrence of eccentric molt in first-year Wrentits at the Palomarin Field Station from 1999 to 2009 ($N = 159$). In years with a positive value, the incidence of eccentric molt was greater than in years with negative values.

fledging date was more important than nestling condition. Because we know of no other studies where the correlation between nestling condition and the extent of molt has been examined, further study is needed.

Postfledging parental care may also play a role. The amount of time spent with dependent young and the quality of that time (i.e., learning crucial life skills) may influence a young bird's ability to obtain enough food to meet the energy demands associated with molt. For example, years when eccentric molt was more common in our study may have coincided with years when more Wrentit pairs were first-time breeders. We know of no studies that have examined the role

of parental care and the incidence and extent of molt. Finally, another explanation for the higher incidence of eccentric molt in certain years is simply measurement error among observers; some individuals may be more likely to detect a molt limit or other evidence of eccentric molt than others. However, given the emphasis on training and standardization of methods, we find this explanation unlikely.

Our results suggest that the occurrence of eccentric molt in first-year Wrentits is more likely to be a response to fledging date than to annual variation in weather. Thus, Wrentits, and potentially other nonmigratory birds, may be limited in their ability to respond

to rapid environmental change by making short-term adjustments in their molt strategies. Such canalization of life history strategies may limit the ability of some birds to respond to rapid climate change, as has been demonstrated in the growing mismatch between breeding and food availability for some migratory birds (Both et al. 2006). Recognizing the importance of molt in a conservation context and developing a better understanding of the environmental constraints on molt may improve our ability to predict the response of birds to a rapidly changing climate.

ACKNOWLEDGMENTS

We thank the many Palomarin field biologists, without whose countless hours in the field this project would not have been possible. We also thank L. R. Mewaldt, D. F. DeSante, and C. J. Ralph for establishing the long-term monitoring program at Palomarin. Conversations with S. Howell and B. Bolker influenced the biological and statistical aspects of our work. S. Howell, G. Geupel, and four anonymous reviewers provided comments that improved the manuscript. Our research was funded by the members and board of directors of PRBO, Chevron Corporation, Bernard Osher Foundation, Gordon and Betty Moore Foundation, Kimball Foundation, National Park Service Inventory and Monitoring Program, and three anonymous donors. Palomarin received exceptionally generous support from the late Dorothy Hunt. Special thanks to the Point Reyes National Seashore and the Golden Gate National Recreation Area for their continued support. Research was conducted at the Palomarin Field Station, which received support from the National Science Foundation (DBI-0533918). This is PRBO contribution number 1772.

LITERATURE CITED

- BALLARD, G., G. R. GEUPEL, AND N. NUR. 2004. Influence of mist-netting intensity on demographic investigations of avian populations. *Studies in Avian Biology* 29: 21–27.
- BATES, D., AND M. MAECHLER [online]. 2009. lme4: Linear mixed-effects models using Eigen and S4 classes. R package version 0.999375–32. Available at: <<http://CRAN.R-project.org/package=lme4>> (29 June 2011).
- BOJARINOVA, J. G., E. LEHIKONEN, AND T. EEVA. 1999. Dependence of postjuvenile moult on hatching date, condition and sex in the Great Tit. *Journal of Avian Biology* 30: 437–446.
- BOLKER, B. M., M. E. BROOKS, C. J. CLARK, S. W. GEANGE, J. R. POULSEN, M. H. H. STEVENS, AND J. S. WHITE. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24: 127–135.
- BOTH, C., S. BOUWHUIS, C. M. LESSELLS, AND M. E. VISSER. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* 441: 81–83.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, NY.
- BUTLER, L. K., T. J. HAYDEN, AND L. M. ROMERO. 2008. Prebasic molt of Black-capped and White-eyed vireos: effects of breeding site and the El Niño–Southern Oscillation. *Condor* 110: 428–440.
- CHASE, M. K. 2002. Nest site selection and nest success in a Song Sparrow population: the significance of spatial variation. *Condor* 104: 103–116.
- , N. NUR, AND G. R. GEUPEL. 2005. Effects of weather and population density on reproductive success and population dynamics in a Song Sparrow (*Melospiza melodia*) population: a long-term study. *Auk* 122: 571–592.
- DAWSON, A. 1998. Photoperiodic control of the termination of breeding and the induction of moult in House Sparrows *Passer domesticus*. *Ibis* 140: 35–40.
- DESANTE, D. F., AND G. R. GEUPEL. 1987. Landbird productivity in central coastal California: the relationship to annual rainfall, and a reproductive failure in 1986. *Condor* 89: 636–653.
- FLANNERY, M. E., AND T. GARDALI. 2000. Incomplete first prebasic molt in the Wrentit. *Western Birds* 31: 249–251.
- GEUPEL, G. R., AND G. BALLARD [online]. 2002. Wrentit (*Chamaea fasciata*). In: *The Birds of North America Online* (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY; Retrieved from the Birds of North America Online: <<http://bna.birds.cornell.edu/bna/species/654>> (4 March 2011).
- , AND D. F. DESANTE. 1990. Incidence and determinants of double brooding in Wrentits. *Condor* 92: 67–75.
- HOWELL, S. N. G. 2010. Molt in North American birds. Houghton Mifflin Harcourt, New York, NY.
- , AND C. CORBEN. 2000. Retarded wing molt in Black-legged Kittiwakes. *Western Birds* 31: 123–125.
- , ———, P. PYLE, AND D. I. ROGERS. 2003. The first basic problem: a review of molt and plumage homologies. *Condor* 105: 635–653.
- JENNI, L., AND R. WINKLER. 1994. Molt and ageing of European passerines. Academic Press, London, UK.
- JONGSOMJIT, D., S. L. JONES, T. GARDALI, G. R. GEUPEL, AND P. J. GOUSE. 2007. A guide to nestling development and aging in altricial passerines. U. S. Department of Interior, Fish and Wildlife Service, Biological Technical Publication, FWS/BTP-R6008–2007, Washington, D.C.
- MARTIN, T. E., AND G. R. GEUPEL. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* 64: 507–519.
- MICHENER, H., AND J. R. MICHENER. 1940. The molt of House Finches of the Pasadena region, California. *Condor* 42: 140–153.
- MICHENER, J. R. 1953. Molt and variations in plumage pattern of mockingbirds at Pasadena, California. *Condor* 55: 75–89.

- MULVIHILL, R. S., AND R. L. WINSTEAD. 1997. Variation in the extent of the first prebasic wing molt of Dark-eyed Juncos. *Journal of Field Ornithology* 68: 183–199.
- NETO, J. M., AND A. G. GOSLER. 2006. Post-juvenile and post-breeding moult of Savi's Warblers *Locustella luscinioides* in Portugal. *Ibis* 148: 39–49.
- PRESTON, K. L., AND J. T. ROTENBERRY. 2006. The role of food, nest predation, and climate in timing of Wrentit reproductive activities. *Condor* 108: 832–841.
- PYLE, P. 1997a. Identification guide to North American birds. Slate Creek Press, Bolinas, CA.
- . 1997b. Molt limits in North American passerines. *North American Bird Bander* 22: 49–89.
- . 1998. Eccentric first-year molt patterns in certain Tyrannid flycatchers. *Western Birds* 29: 29–35.
- , A. McAndrews, P. Veléz, R. L. Wilkerson, R. B. Siegel, AND D. F. DESANTE. 2004. Molt patterns and age and sex determination of selected southeastern Cuban landbirds. *Journal of Field Ornithology* 75: 136–145.
- R Development Core Team [online]. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: <<http://www.R-project.org>> (29 June 2011).
- ROTENBERRY, J. T., AND J. A. WIENS. 1991. Weather and reproductive variation in shrubsteppe sparrows: a hierarchical analysis. *Ecology* 72:1325–1335.
- SILKEY, M., N. NUR, AND G. R. GEUPEL. 1999. The use of mist-net capture rates to monitor annual variation in abundance: a validation study. *Condor* 101: 288–298.
- WILSON, S., AND P. ARCESE. 2003. El Niño drives timing of breeding but not population growth in the Song Sparrow (*Melospiza melodia*). *Proceedings of the National Academy of Sciences USA* 100:11139–11142.
- ZUUR, A. F., E. N. IENO, N. J. WALKER, A. A. SAVELIEV, AND G. M. SMITH. 2009. Mixed effects models and extensions in ecology with R. Springer, Berlin, Germany.