

Phenology and sequence of the complete prealternate molt of Bobolinks in South America

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ABSTRACT. Molt phenology plays an important role in the annual cycles and energetic budgets of migratory birds. The timing and sequence of molt of Nearctic-Neotropical migratory passerines is generally known for species that undergo a complete prebasic molt on or near the breeding grounds. However, for the few passerine species such as Bobolinks (*Dolichonyx oryzivorus*) that undergo a complete prealternate molt, the phenology of this molt on the wintering grounds has received little attention. Most studies evaluate prebasic molt, often carried out in conjunction with a different set of competing energetic demands and under dramatically different conditions (e.g., climate and food availability). The prebasic molt of Bobolinks has been described based on limited museum collections, but the sequence and phenology of the prealternate molt have not been examined. We collected molt data from 242 Bobolinks captured from January to March in Bolivia (2005–2007) and Argentina (2008). We quantified prealternate molt sequence and used a maximum likelihood approach to estimate molt initiation date and duration. We used AIC model selection to evaluate the potential effects of region, year, and sex on prealternate molt phenology. Onset and duration of molt did not differ among years or between males and females. Estimated molt duration was 13 d longer at Bolivia sites than at sites 1200 km further southeast in Argentina, but molt duration in Argentina varied and the difference was not statistically significant. Molt sequence was consistent among populations, and showed only slight deviations from what has been previously reported for Bobolinks. Our results suggest that regional wintering populations of Bobolinks do not mix in a given year, and local factors such as climate and food availability may influence molt phenology.

RESUMEN. El ritmo y secuencia de la muda prealterna completa de *Dolichonyx oryzivorus* en Sudamérica

El ritmo de la muda juega un rol importante en los ciclos anuales y en el reparto energético de las aves migratorias. El ritmo y secuencia de la muda de aves migratorias Nearcticas-Neotropicales del orden Passeriformes es generalmente conocido para especies que tienen una muda prebásica completa en o cerca de su distribución reproductiva. Sin embargo, para las pocas especies de passeriformes como *Dolichonyx oryzivorus* que tienen una muda prealterna completa, el ritmo de esta muda en su distribución no-reproductiva ha recibido poca atención. La mayoría de los estudios evalúan la muda prebásica, cual es a menudo realizado simultáneamente con un grupo de gastos energéticos diferentes, y bajo condiciones dramáticamente diferentes (ej., clima y disponibilidad de comida). La muda prebásica de *D. oryzivorus* ha sido descrita en base de una limitada serie de colecciones de museo, pero la secuencia y el ritmo de la muda prealterna no han sido examinadas. Colectamos datos de muda de 242 *D. oryzivorus* capturados desde Enero hasta Marzo en Bolivia (2005–2007) y Argentina (2008). Cuantificamos la secuencia de la muda prealterna y usamos un método de máxima verosimilitud para estimar la fecha de la iniciación de la muda y su duración. Usamos el Criterio de Información de Akaike para seleccionar modelos y evaluar los efectos potenciales de la región, año y sexo sobre el ritmo de la muda prealterna. El inicio y la duración de la muda no varió entre años o entre machos y hembras. La duración estimada de la muda fue 13 días mas largo en sitios en Bolivia que en sitios 1200 km al sudeste en Argentina, pero la duración de la muda en Argentina varió y la diferencia no fue estadísticamente significativa. La secuencia de la muda fue consistente entre poblaciones y demostró solo una leve variación de lo que se ha reportado previamente para *D. oryzivorus*. Nuestros resultados sugieren que las poblaciones regionales de *D. oryzivorus* de la época no-reproductiva no se mezclan en un año dado, y que factores locales como el clima y la disponibilidad de comida podrían influenciar el ritmo de la muda.

Key words: Argentina, Bolivia, *Dolichonyx oryzivorus*, molt phenology, molt sequence, South America

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Understanding molt strategies and the plasticity of molt phenology enhances our ability to interpret ecological, physiological, and temporal constraints imposed on bird populations during different parts of their annual cycle. Molting is energetically costly and temporal overlap with activities such as reproduction and migration is usually minimal (Jenni and Winkler 1994). Molt strategies reflect trade-offs among these other demands and can vary within species (Jenni and Winkler 1994) and among years (Salewski et al. 2004). The behavioral ecology of a species and factors such as climate, habitat, and resource availability influence the rate, timing, and extent of molt (Rohwer et al. 2005).

Bobolink (*Dolichonyx oryzivorus*) is one of two North American bird species known to undergo two complete annual molts: a prebasic molt in North America and a prealternate molt on the wintering grounds in South America. Svensson and Hedenström (1999) suggested that exposure to UV rays may accelerate feather wear in open-habitat species (like Bobolink), precipitating the need for two molts per year. Barta et al. (2008) suggested that abundant food supplies allow for two complete molts of relatively low-quality feathers (as opposed to one molt of high-quality feathers), precipitating rapid feather wear and a need for replacement biannually. Franklin's Gull (*Larus pipixcan*), although taxonomically distant from Bobolink, also undergoes a complete molt twice annually. As Howell (2010) pointed out, both species have similar life history traits that underlie their parallel molt strategies: they are long-distance migrants exposed to the sun in open habitats during both summer and winter, resulting in substantial feather wear, and they winter at latitudes in South America where food is abundant, presumably providing the energy needed to molt before spring migration.

Undergoing two complete molts per cycle is advantageous for polygynous species like Bobolink. Fresh plumage in spring may enhance the ability of males to advertise to females and conspecific males (Tökölyi et al. 2008). Because Bobolinks are sexually dimorphic and males use flight displays to attract mates, feather quality can be an important predictor of pairing success (Mather and Robertson 1992). Longer periods of molt can result in higher feather quality (Dawson et al. 2000, Hall and Fransson 2000, Gordo 2007), and, conse-

quently, a higher quality phenotype (Serra et al. 2007). The duration of Bobolink prealternate molt on the wintering grounds may therefore have consequences on the breeding grounds.

Descriptions of molt sequence for Bobolinks appear to be based primarily on specimens collected in North America during prebasic molt (Jones 1930). The timing and sequence of prealternate molt in wintering Bobolinks have not been described (Martin and Gavin 1995). Our objectives were to describe molt sequence and assess variability in phenology over multiple years in two wintering areas. We evaluated the molt sequence of flight feathers, coverts, and contour feathers, and focused on the primary feathers to assess molt onset and duration. We hypothesized that geographically distinct wintering Bobolink populations would differ in molt initiation date or duration, presumably due to differences among regions in environmental conditions such as climate, food, and day length that affect molt.

METHODS

We collected molt data in Bolivia from 2005 to 2007 at nine sites within 300 km of each other (15°45'41"S, 64°09'27"W), and at two sites in Argentina in 2008 (25°55'28" S, 58°32'06"W, maximum distance between sites = 7 km; Fig. 1). Bolivian and Argentinean sites were located near the northernmost limit and in the southern part of the Bobolink's winter range, respectively. The distance between the Argentina and Bolivia sites was >1200 km, and the latitudinal difference was 10°. Bolivian sites consisted of rice plantations and adjacent idle fields that were used by Bobolinks as day or night roosts. Argentinean sites were reed marshes with irregular openings colonized by grasses and other herbaceous vegetation associated with the permanently flooded areas of the marsh and its edges. Bobolinks used the marshes, and especially the clearings within them, for roosting as well as for daytime feeding.

In 2007 and 2008, El Niño and La Niña affected areas within the Bobolink wintering range. Bobolink flocks were dramatically reduced in size at Bolivia sites in 2007, when precipitation in January and February was approximately 50% higher than during the same months the two previous

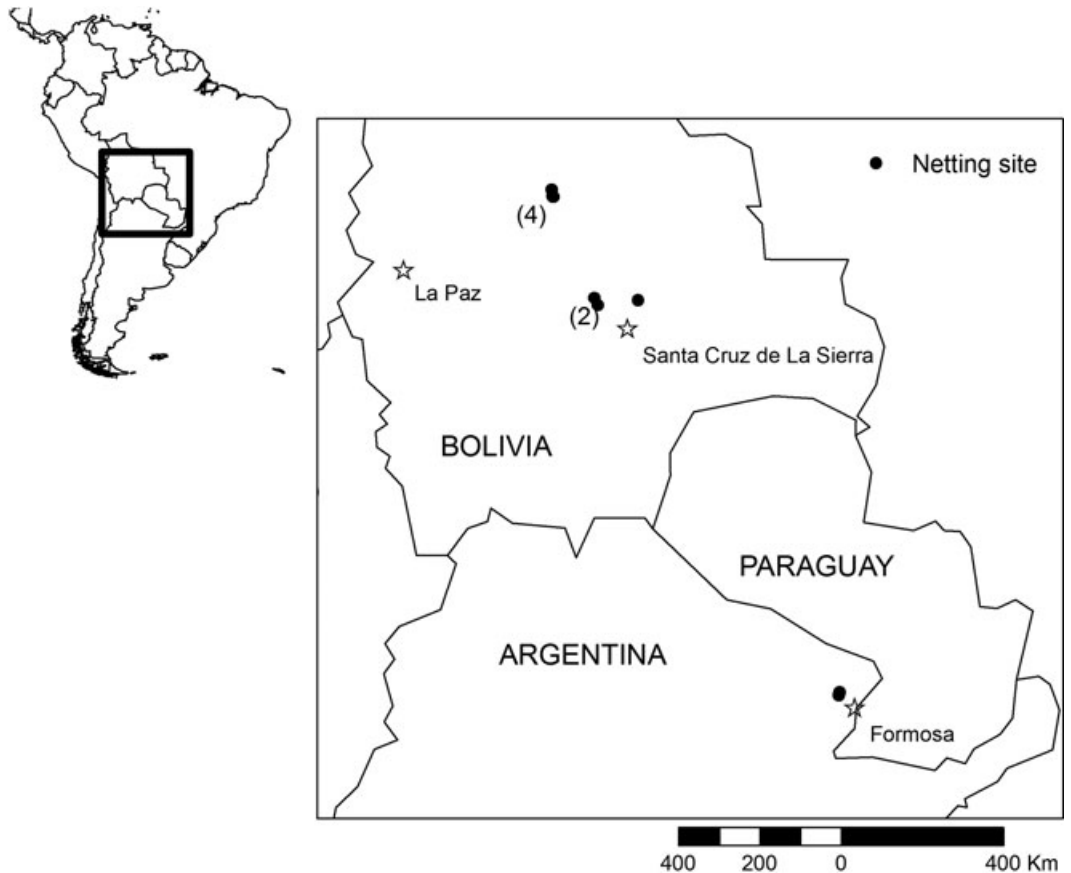


Fig. 1. Sites in Bolivia (2005–2007) and Argentina (2008) where Bobolinks were captured in mist nets. Data from sites within 2 km of each other (number in parentheses) are combined.

years (Tutiempo Network 2009). In Formosa, Argentina, precipitation was 2.5 times higher in 2007 and 2008 than in 2005 and 2006 (Tutiempo Network 2009).

Bird capture and molt scoring. We captured Bobolinks using mist nets at day roosts, night roosts, and foraging areas. Because Bobolinks are highly mobile on the wintering grounds, we adopted an opportunistic capture strategy. Bobolinks generally move along consistent pathways between day foraging areas and roosts. We typically used one to five nets placed strategically to intercept flight pathways, or within roost and feeding sites.

We scored molt for 242 Bobolinks (146 males and 96 females). In Bolivia, we collected molt data from Bobolinks captured between 22 January and 6 March over 3 yr (2005: $N = 40$; 2006: $N = 137$; 2007: $N = 21$).

Dates of collection varied among years: 7–18 February in 2005, 25 January–6 March in 2006, and 23–26 January in 2007. In Argentina, we collected molt data from 44 Bobolinks (23 males, 21 females) between 20 January and 4 February 2008; recordings of Bobolink calls were sometimes used to increase capture rates. We captured 40 Bobolinks at one site, and another four Bobolinks at a site 7 km away. All but three individuals were actively molting primary feathers on both wings (one had begun molt on one wing, one had nearly completed molt, and one had only begun contour feather molt). Detailed molt data were collected for all birds captured in Argentina, but when large numbers of simultaneous captures sometimes occurred in Bolivia, we limited handling time by collecting molt data on a random subset of individuals.

We recorded standard morphometric measurements and marked each Bobolink with a unique USGS aluminum band. Sex was determined strictly by plumage because all birds had begun growing contour or flight feathers. Wing chord was often not an accurate way to determine sex because old P9 feathers often showed considerable wear. We used a conventional molt scoring system (Ginn and Melville 1983) that assigns each remex a score from 0 to 5 (0 = old feather present, 1 = feather missing or in pin, 2 = feather emerged from pin and up to one-third grown, 3 = feather one-third to two-thirds grown, 4 = feather two-thirds to nearly full-grown, and 5 = new feather fully grown). For all birds, molt was recorded for primary, secondary, and tertiary flight feathers on both wings, and primary coverts on the right wing. We created molt summary tables following Rohwer (2008). Direction of growth between feathers was identified as proximal or distal, and growing feathers were defined as nodal or terminal based on neighboring feathers. Molt scores for greater coverts on the right wing were recorded only for birds captured in Argentina. Molt of the body feathers (head, dorsal, and ventral) and lesser and median coverts were coded based on stage and intensity of molt. Values ranged from 0 to 50, with the first number representing the predominant stage of feather growth, based on the same 0–5 scale used for flight feathers, and the second number corresponding to the proportion of feathers molting (0 = no molt, 1 = light molt, 2 = moderate molt, and 3 = heavy molt). To display timing of molt, we categorized extent of molt of the primaries, secondaries, and rectrices (Willoughby 1986) as 0, 1, or 2 (0 = no feathers molting on either wing/side, 1 = at least one feather molting on at least one wing/side, and 2 = at least one feather in active molt on both wings/side). We disregarded the 10th (vestigial) primary feather.

Analysis. To estimate molt initiation date and duration, we used data from birds that were actively molting primary feathers and for which we had primary molt data from both wings ($N = 236$). Scores were calculated using both wings (score range = 1–89). The relationship between primary molt score and time is often not linear, and one way to address this problem is to use the rate of feather growth via percent feather-mass (weight per unit length) grown rather than the score described above

(Underhill et al. 1990, 1992, Underhill and Zucchini 1988, Dawson 2003). However, Underhill and Zucchini (1988) suggested that this is less problematic for passerines. For our Bobolink data, inspection of the raw molt scores over time depicted a linear function and, when we fitted linear and quadratic models, we found no difference in variance explained based on adjusted R -squared values. We concluded that using feather mass would therefore have a negligible influence on results.

To estimate initiation date and molt duration using molt score data without repeat captures, it is convention to regress date on molt (Pimm 1976). However, two key model assumptions are not met with this traditional approach: (1) that dates of data collection are random (in practice they are not random because the observer chooses when to sample), and (2) residuals are heteroscedastic (Underhill and Zucchini 1988). To meet these assumptions, we used a maximum likelihood approach for data on birds in active molt (“Type 3” molt; Underhill and Zucchini 1988). All birds captured had initiated molt; birds at Argentina sites were all actively molting, and individuals at Bolivia sites that had completed molt (in 2006 when sampling continued into March) were not included in the analysis. We estimated molt initiation and duration at Bolivia and Argentina sites separately to permit comparison of estimates at these disparate locations.

We compared *a priori* models estimating molt duration for molt data collected in Bolivia (2005–2007): (1) Null, (2) Sex effect, and (3) Year effect. For the Argentina sites, we tested for a sex effect. We also evaluated a model that included a region effect (Bolivia vs. Argentina sites). To evaluate models that included a region, sex, or year effect, we summed the maximized log-likelihood values from separate submodels (e.g., for a model that included sex as a parameter, the likelihood value for males plus the likelihood value for females) and compared it to the maximum log-likelihood for the combined data set (e.g., data for both males and females; *sensu* Salweski et al. 2004). Models were compared using Akaike Information Criteria adjusted for sample size (AICc); the model with the smallest AICc value was the most parsimonious representation of the data, and models with $\Delta\text{AICc} < 4$ would be considered plausible (Burnham and Anderson 2002). We calculated Akaike weights

to assess the relative support for each model from the data. For all analyses, we used program R (R Development Core Team 2008).

RESULTS

Sequence of the complete prealternate molt. The general sequence of prealternate molt in Bobolink feather tracts followed a consistent pattern (Tables 1 and 2). Primary molt began with the innermost primary (P1) and primary covert, with replacement proceeding sequentially from proximal to distal (Fig. 2). The lesser and underwing coverts began molt at about the same time. Replacement of feathers on the head, underparts, and upperparts usually began shortly after the inner primaries, and finished after all primaries were completed. Initiation of tertial molt coincided with P4. Molt of the secondaries began when P5–P6 were replaced. The greater coverts molted simultaneously, following P4 and just before the secondaries began molting. The median coverts were replaced at the same time as P5–P6. Commencement of tail, scapular, and alular molt corresponded with molt of the outer primaries. The tail molted in quick succession as early as the end of January (Fig. 2), starting with the inner rectrices (R1) and proceeding centrifugally (Table 2). The sequence of flight feather molt was bilaterally symmetric for both males and females.

Onset of contour feather molt occurred from late January through March (Fig. 3). Most individuals commenced molt in the head region. Upper and underparts generally molted throughout late January–March, although underparts showed a slightly more pronounced progression of molt throughout the molt period. Underwing feathers did not show a clear pattern; some individuals retained underwing feathers as late as March, whereas others were molting them in late January. Scapulars were old on most individuals captured from late January to early March, after which they were either at some stage of molting or replaced. Birds captured in Bolivia started molting scapulars later than birds from Argentina. Scapular molt proceeded from the shoulder region towards the back.

Molt onset and duration. Estimated molt initiation dates were similar in Argentina and Bolivia, but estimated molt duration was 13 d shorter in Argentina (Table 3, Fig. 4). However,

confidence intervals for molt duration in Bolivia and Argentina overlapped (95% CI: BOL = 50.14, 63.86 d; AR = 29.69, 58.31 d), and the null model was more parsimonious ($AIC_c = 352.7$) than the model with region included as a factor ($AIC_c = 373.5$). The estimated dates of molt completion for Bobolinks in Bolivia and Argentina were 1 March and 19 February, respectively.

Models with the lowest AIC_c values for Bobolink molt initiation date and duration in Bolivia did not include year or sex (Table 4). In Argentina, where Bobolinks were captured during only one season, we found no evidence that molt initiation or duration differed between males and females.

DISCUSSION

Sequence of the complete prealternate molt. The prealternate molt sequence in Bobolinks follows what has generally been observed in passerines (Ginn and Melville 1983, Pyle 1997), and was consistent among individuals. For some individuals, middle secondaries were retained after molt of other secondary feathers. Specifically, 14 individuals from Bolivia retained two to three middle/inner secondaries while in the process of replacing the others; one bird had almost fully replaced S1, 2, and 6 without any sign of molting S3, 4, or 5. However, we do not know if these individuals retained secondaries until the following prebasic molt or molted them after release. Inner secondaries are infrequently retained during Bobolink prebasic molt, and sometimes in SY birds during the prealternate molt (Pyle 1997). Data from Bobolinks captured in Vermont suggest that this phenomenon is rare, that is, 0 of 332 Bobolinks captured in May (2002–2008) showed retention of inner secondaries in the prealternate molt (N. Perlut, pers. comm.).

Prealternate molt in Bobolinks has not previously been documented in detail, and few data exist for comparison with the molt patterns we observed. Jones (1930) provided limited documentation based on museum specimens, but did not indicate how many specimens were analyzed nor whether he evaluated individuals in prebasic, prealternate, or both molts. We were unable to directly compare our results with his observations, given our different methods. Jones (1930) grouped the greater coverts with

Table 1. Count summary of the raw molt scores for primaries (P1–P9) and secondaries (S1–S9) for Bobolinks ($N = 242$) in Bolivia and Argentina. Iterated summary data have been adjusted to account for the fact that wing quills are split into three molt series, S9–S7, S6–S1, and P1–P9, separated by the gray bars (*sensu* Rohwer 2008).

	Secondaries									Primaries								
	S9	S8	S7	S6	S5	S4	S3	S2	S1	P1	P2	P3	P4	P5	P6	P7	P8	P9
Raw summary data																		
Nodal	2	54	3	0	3	11	0	0	0	105	6	0	0	0	0	0	0	0
Direction ← (prox)	102	5	0	0	3	11	84	100	135	0	0	0	0	0	0	0	0	1
Direction → (distal)	4	124	131	37	5	0	0	0	0	0	15	41	73	94	139	110	59	0
Direction?	4	2	0	22	37	2	5	1	0	7	1	3	5	1	1	7	23	0
Terminal	16	2	0	4	29	24	0	0	0	0	0	0	0	0	0	0	19	77
No. growing	80	61	77	59	51	49	71	76	89	16	19	39	66	83	94	90	82	70
Iterated summary data																		
Nodal	2	54	3	35	2	0	0	1	86	15	6	0	0	0	0	0	0	0
Direction ← (prox)	102	5	3	3	11	84	100	135	0	0	0	0	0	0	0	0	0	1
Direction → (distal)	4	124	37	37	5	0	0	0	0	15	41	73	94	130	139	110	59	0
Direction?	4	2	22	37	2	5	1	0	7	1	3	5	1	1	7	23	0	0
Terminal	15	2	56	4	29	24	0	0	0	0	9	0	0	0	0	0	19	77
No. growing	80	61	77	59	51	49	71	76	89	16	19	39	66	83	94	90	82	79

Table 2. Count summary of raw molt scores for rectrices of Bobolinks ($N = 242$) in Bolivia and Argentina. Iterated summary data have been adjusted to account for the fact that rectrices are split into two molt series by side (right and left) separated by the gray bar.

	Left						Right									
	R6	R5	R4	R3	R2	R1	R1	R2	R3	R4	R5	R6				
Raw summary data																
Nodal	3	0	0	0	1	18	0	4	1	0	16	2	0	1	0	2
Direction ←	38	26	0	16	11	21	0	4	2	1	16	2	0	1	1	2
Direction →	3	0	0	1	0	1	5	19	16	15	21	37	0	21	37	0
Direction ?	50	60	68	68	75	66	79	63	70	69	67	50	0	67	50	0
Terminal	54	16	0	0	0	0	0	0	0	0	3	0	0	1	11	48
No. growing	89	84	82	83	84	85	81	81	85	82	81	85	85	85	86	88
Iterated summary data																
Nodal	3	0	0	0	7	25	24	4	10	0	24	10	0	0	1	2
Direction ←	38	26	0	16	11	21	24	4	10	0	24	10	0	0	1	2
Direction →	3	0	0	1	0	1	24	19	16	15	21	37	0	21	37	0
Direction ?	50	60	68	68	75	66	79	63	70	69	67	50	0	67	50	0
Terminal	54	16	0	0	0	0	0	0	0	0	5	1	0	1	11	48
No. growing	89	84	82	83	84	85	81	81	85	82	81	85	85	85	86	88

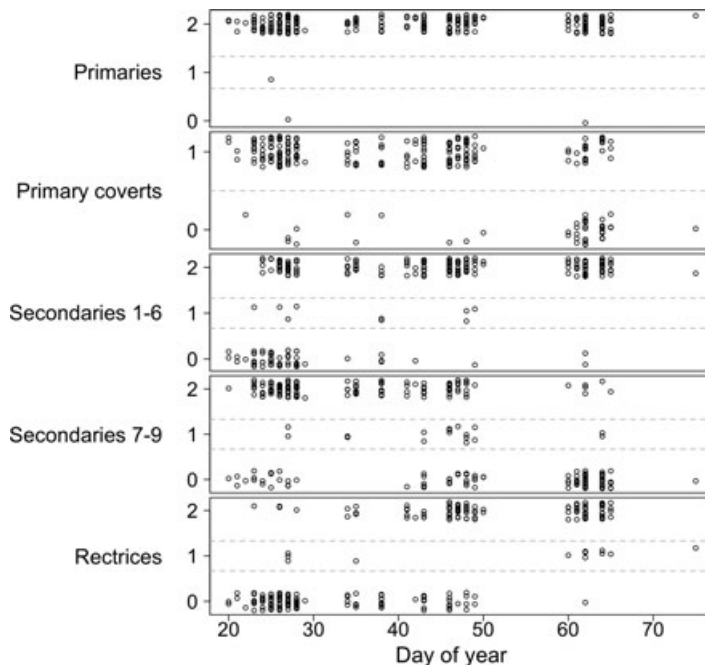


Fig. 2. Timing of molt of flight feather tracts (primaries, secondaries, and rectrices) and primary coverts for Bobolinks ($N = 242$) in Argentina and Bolivia. Molting categories for the primaries, secondaries, and rectrices are: 0 = no molt on either wing/side, 1 = at least one feather molting on at least one wing/side, and 2 = at least one feather in active molt on both wings/sides (Willoughby 1986). Molt codes for the primary coverts are: 0 = no molt; and 1 = at least one feather on the right wing is actively molting. Overlapping points within each molt category are jittered. Dotted gray lines divide the molt categories. Day of year run from 20 January (20) to about 16 March (75).

the inner primaries and labeled it as the first group to molt. Our data indicate that, for some individuals, greater covert molt does not start with the replacement of the innermost primaries, but rather with P5–P6, when the secondaries begin to molt. Molt onset for most feather tracts was consistent in both regions in our study, but onset of scapular molt was later in Bolivia, perhaps due to the more protracted nature of molt at those sites.

Molt onset and duration. Wintering Bobolinks molted between the first week of January and the first week of March. Analysis of geolocator data show three Bobolinks arriving in Argentina and Paraguay between 17 December and 18 January (R. Renfrew, unpubl. data). Assuming these individuals are representative of most Bobolinks, molt begins within 3 weeks of arrival on the wintering grounds, and immediately for late-arriving individuals. Our data corroborate other evidence suggesting that

Bobolink populations in Bolivia and Argentina, though potentially mobile, do not mix during the winter months of January through March. We found Bobolinks in all stages of molt in both countries, and found a difference, although not significant, in molt duration between the two countries. Bobolinks are present in both areas throughout the winter (Renfrew and Saavedra 2007, Di Giacomo et al. 2008), and geolocator data analyzed to date provide no evidence that individuals undertake major movements during the molt period (R. Renfrew, unpubl. data).

Our data lend evidence to the rarity of prealternate molt suspension in Bobolinks (Pyle 1997). In South America, all 498 Bobolinks captured over 4 yr had initiated molt by February (R. Renfrew, unpubl. data). In Vermont, only one of 332 Bobolinks captured in May (2002–2008) had suspended molt (N. Perlut, pers. comm.). The costs of a suspended prealternate molt in Bobolinks include migrating with worn

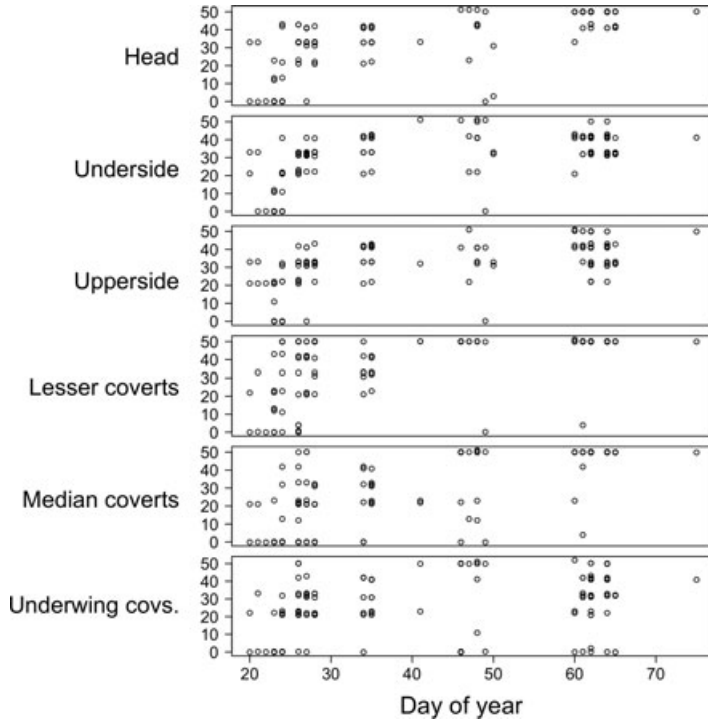


Fig. 3. Molt timing of body feathers as well as lesser, median, and underwing coverts for a subset (144) of Bobolinks caught in Argentina and Bolivia. The y-axis displays the molt scores from 0 to 50 (representing a gradient in molt intensity). The first number represents the predominant stage of feather growth, based on the same 0–5 scale used for flight feathers; the second number corresponds to the proportion of feathers molting (1 = light molt, 2 = moderate molt, and 3 = heavy molt), with 0 = no molt present and 50 = all new feathers/molting complete. Day of year run from 20 January (20) to 16 March (75).

feathers and expending energy on molt at the same time that territories are being established.

Passerine molt research has focused primarily on the complete prebasic molt and its association with events during the breeding season (Rohwer et al. 2005), and potential factors influencing complete prealternate molt during winter cannot be surmised from this work. Nonetheless, some universal concepts apply, and studies on trans-Saharan migrant passerines offer comparative context for a long-distance Nearctic-Neotropical migrant like Bobolink.

Molt duration in Argentina fits within the typical range for long-distance migrants (Ginn and Melville 1983), but was shorter than the prebasic molt of most migratory passerines. Bobolink prealternate molt might be expected to take longer than prebasic molt, given that the latter must be carried out within the constraints imposed by the energetically demanding activities of breeding and fall migration (Jenni and Winkler 1994). For example, Willow Warbler (*Phylloscopus trochilus*), the only trans-Saharan migrant passerine that undergoes a complete

Table 3. Estimated molt initiation date, standard deviation of initiation, and duration (days) of primary feather molt for Bobolinks in Bolivia and Argentina. Standard errors are in parentheses.

Location	N	Initiation date	SD of initiation date	Duration
Bolivia	193	4 January (2.1)	8 (0.5)	57 (3.5)
Argentina	43	7 January (3.7)	5 (1)	44 (7.3)

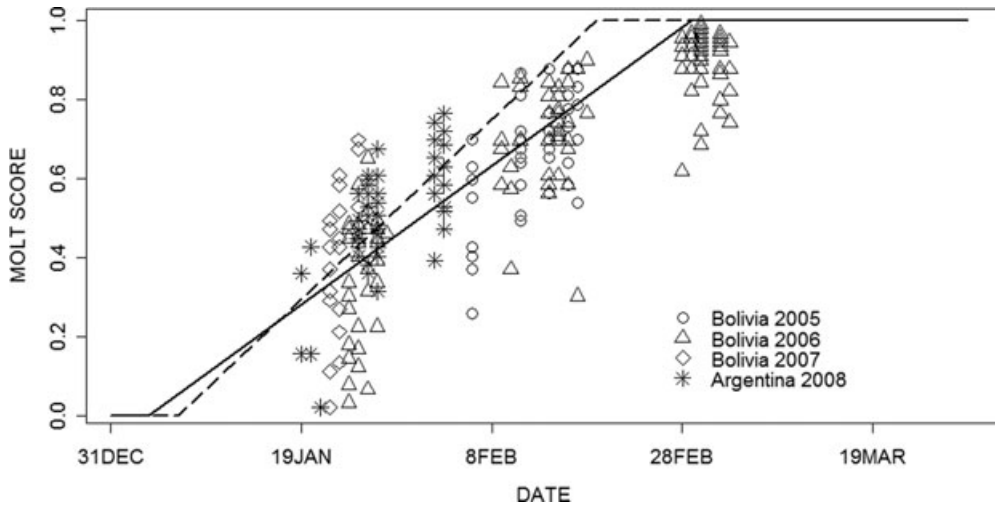


Fig. 4. Prealternate molt scores for Bobolinks captured in South America. The solid and dashed lines represent the estimated timing and duration of molt for Bobolinks captured at Bolivia (2005–2007) and Argentina (2008) sites, respectively.

molt twice each year, complete their prebasic molt in 37 d (Ginn and Melville 1983) and their prealternate molt in 50–68 d (Underhill et al. 1992), respectively. To our knowledge, no estimates of prebasic molt duration in individual Bobolinks exist for comparison with our data.

Molt strategies of each species are shaped by life-history traits such as migration distance (Hall and Tullberg 2004), habitats used that may influence feather deterioration (Rohwer et al. 2005), and latitude (e.g., Underhill et al. 1992). External factors that influence molt include climate and related food availability, and events during other parts of the life cycle (Ryder and Rimmer 2003, Butler et al. 2008, Howell 2010). Intraspecific and interannual variation in molt phenology and extent can be plastic (Pyle et al.

2009), and associated with ultimate factors such as general climatic conditions and events (Heise and Rimmer 2000, Butler et al. 2008), which can influence proximate factors such as food availability (Barta et al. 2008, Tökölyi et al. 2008), and precise timing of reproduction (e.g., Heise and Rimmer 2000; see Howell 2010 for a review of factors). Causation, however, can be challenging to verify (Salewski et al. 2004).

Migration distance may be associated with phylogenetic variation in molt phenology (Norman 1997, Svensson and Hedenström 1999, Tökölyi et al. 2008), but is not believed to be a primary, underlying mechanism (Rohwer et al. 2005). Among wintering populations of Bobolinks, however, the distance migrated may be associated with arrival date on the wintering

Table 4. Models of primary feather molt timing and duration for Bobolinks at wintering sites in Argentina and Bolivia. For Bolivian sites, we compared three *a priori* models depicting a sex effect, year effect, and a null model. For Bobolinks in Argentina, we compared a sex effect model and a null model. The most parsimonious model has the lowest AIC value.

Location and years	Model	K	AIC _c	ΔAIC _c	Weight
Bolivia (2005–2007)	Null (no difference in molt among yrs or between males and females)	3	312.9	0.0	1.0
	Difference between males and females	6	319.4	6.5	0.0
	Difference among yrs	9	328.8	15.9	0.0
Argentina (2008)	Null (no difference between males and females)	3	73.0	0.0	1.0
	Difference between males and females	6	86.8	13.8	0.0

grounds, which may in turn influence molt initiation and duration. Three Bobolinks with geolocators reached stopover sites in Bolivia in November before continuing southeast to their wintering grounds in Argentina and Paraguay (R. Renfrew, unpubl. data), suggesting that birds wintering in Bolivia could arrive as early as November. The tendency for Bobolinks wintering in Bolivia to have a more protracted molt may reflect their earlier arrival compared to individuals wintering 1200 km further southeast in Argentina. However, birds that arrived in Argentina (near the presumed southern edge of the species' wintering range) in late December or January remained there for 3–3.5 months, long enough to allow them to grow quality feathers (Dawson et al. 2000, Hall and Fransson 2000, Gordo 2007). This suggests that date of arrival on the wintering grounds may not affect molt duration.

Bobolink prealternate molt duration may be influenced by local climatic conditions, particularly precipitation (Butler et al. 2008). Although precipitation does not always influence general molt strategy (e.g., Underhill et al. 1992), precipitation can alter the timing of molt on the breeding grounds (Butler et al. 2008), and the onset of dry seasons can hasten molt on the wintering grounds (Bensch et al. 1991). Bobolinks winter in central South America during the rainy season, when occasional widespread inundation of cultivated and noncultivated fields may limit seed availability (R. Renfrew, pers. obs.). Food resources are thought to be important to molt phenology (Tökölyi et al. 2008) and potentially depend on environmental factors such as rainfall (Bensch et al. 1991). If precipitation limits food resources in this system, we would have expected a relatively short and rapid molt in areas with high precipitation, such as at our sites in Bolivia in 2007. Salewski et al. (2004), however, found that molt of three Palearctic passerine migrants occurred throughout the dry season, and factors other than resource abundance may determine molt dynamics. The mobility and diet plasticity of Bobolinks in winter (Renfrew and Saavedra 2007) may buffer the species against potential food limitations associated with climatic conditions.

Our two study regions differed by 10° in latitude, and day lengths at our Argentina study sites were approximately 75 min (early January) to 45 min (late January) minutes longer, respec-

tively, than at our Bolivia sites. As the austral summer progresses, day length shortens more rapidly at the Argentina sites and, by the end of February, differs little from Bolivia sites. Molting in Argentina may be slightly advantageous because feather synthesis is less costly during daylight hours (Murphy and King 1991). Longer day lengths may also promote higher food quality and abundance and enable birds to grow quality feathers more quickly.

The predominant food resources available to wintering Bobolinks differed between our two study regions. Bolivia sites were in agricultural, rice-producing regions where Bobolinks were usually observed feeding on rice (R. Renfrew, pers. obs.). Argentina sites were located in a grassland-dominated landscape, and Bobolinks were usually observed feeding in grasses (S. Frey and J. Klavins, pers. obs.). The availability and nutritional content of food consumed by Bobolinks may differ between these landscapes, with the potential to influence regional-scale molt phenology. A relatively limited, ephemeral, or lower-nutrition food supply may precipitate a faster molt, as observed in birds molting during or preceding drought conditions (Bensch et al. 1991).

The tendency for molt to be shorter for Bobolinks in Argentina could represent a sampling effect if birds were sampled during a different molt stage than birds in Bolivia. However, sample dates varied in our study and sometimes were nonoverlapping within Bolivia sites as well, yet there was no year effect, suggesting that the stage of molt did not influence duration estimates.

Conservation applications. As one of the longest-distance migratory passerine species, the Bobolink is potentially vulnerable to changes in climate over a broad scale (e.g., Cotton 2010, Végvári et al. 2010). Inadequate food resources could delay migration, impair body condition at departure, and limit feather quality, any of which might hinder their ability to respond to changing conditions (Gordo 2007). Advancing arrival on the breeding grounds is one strategy used to adjust to climatic changes, but both short- and long-distance migrants that undergo a prebreeding molt or molt flight feathers on the wintering grounds are less likely to advance arrival than species without any prebreeding molt (Végvári et al. 2010). Changes in molt may signal potential impacts or adjustments to

external factors, necessitating a more thorough understanding of Bobolink molt dynamics.

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