REPLACEMENT SEQUENCE FOR THE FLIGHT FEATHERS OF THE BLUE-BLACK GRASSQUIT (*VOLATINIA JACARINA*) AND THE GRAY SEEDEATER (*SPOROPHILA INTERMEDIA*)

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Abstract.— Knowing the order and way in which the flight feather replacement process takes place is fundamental to elucidate the specific strategies adopted by different species in relation to the environmental and ecological pressures to which they are subjected. This information is not available for the majority of the Neotropical species, which hinders understanding this process in functional or evolutionary contexts. Seeking to determine the replacement sequence of flight feathers during a complete molt in the Blue-black Grassquit (*Volatinia jacarina*) and the Gray Seedeater (*Sporophila intermedia*), captures were made with mist nets at the Centro Universitario Regional del Norte in Universidad del Tolima (Armero-Guayabal, Tolima, Colombia). A standardized protocol was followed for the description and analysis of the molt patterns of flight feathers. In general, the replacement pattern of flight feathers proceeds according to the basic sequence observed in other passerines. Primary remiges in both species constituted a single molt series, as the rectrices. Secondary remiges represent two molt series, which may be related to aerodynamic or energetic necessities. Given the high energetic demands of molting, it might be possible that similar species may evolve different mechanisms to carry on this event, supporting a high phenotypical plasticity among and within lineages, which may be associated with a fast adaptation process.

Key words: *basic sequence, flight feather molt, Magdalena valley, molt pattern.*

Resumen. Secuencia de reemplazo de las plumas de vuelo en el Volatinero (*Volatinia jacarina*) y el Corbatita Gris (*Sporophila intermedia*).— El conocimiento del orden y la forma en que se lleva a cabo el proceso de reemplazo de plumas de vuelo es fundamental para dilucidar las estrategias particulares adoptadas por diferentes especies en relación con las presiones ambientales y ecológicas a las que se encuentran sometidas. Esta información no se encuentra disponible para la mayoría de las especies neotropicales, lo que dificulta la comprensión de este proceso en contextos funcionales o evolutivos. Con el objetivo de determinar la secuencia de reemplazo de las plumas de vuelo durante una muda completa en el Volatinero (*Volatinia jacarina*) y el Corbatita Gris (*Sporophila intermedia*), se realizaron capturas con redes de niebla en el Centro Universitario Regional del Norte de la Universidad del Tolima (Armero-Guayabal, Tolima, Colombia). Se siguió un protocolo estandarizado para la descripción y el análisis de los patrones de muda de las plumas de vuelo. En general, el patrón de reemplazo de las plumas de vuelvo procedió según la secuencia básica observada en otros Passeriformes. Las rémiges primarias en ambas especies constituyeron una única serie de muda, al igual que las rectrices. Las rémiges secundarias representaron dos series, lo que podría estar relacionado con alguna necesidad aerodinámica o energética. Dada la alta demanda energética del proceso de muda, es posible que especies similares desarrollen distintos mecanismos para sobrellevarla, mostrando una alta plasticidad fenotípica entre y dentro de los linajes, lo cual podría estar asociado a procesos de adaptación rápida.

Palabras clave: *muda de plumas de vuelo, patrón de muda, secuencia básica, valle del Magdalena.*

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The detailed study of bird plumage characteristics and thorough description of the patterns and mechanics of the molt process have permitted clearing up temporal and spatial dynamics in the life cycles of a vast amount of birds from temperate zones over the years (Jenni and Winkler 1994, Pyle 1997a, 2008). Sequential replacement of flight feathers, for example, allows many birds to maintain their flight capacity almost intact while they molt (Shugart and Rohwer 1996); consequently, knowing the order and way in which this process takes place is fundamental to elucidate the specific strategies adopted by different species in relation to their natural history and evolution.

Ginn and Melville (1983) denominated as "basic sequence" the replacement sequence of flight feathers most observed in birds, where primaries are molted in distal direction, beginning from P1 and ending in P9–P10. The secondaries are molted in proximal direction, from S1 to S6, while S7–S9 are generally replaced after starting the molt of primaries and a tendency exists where S8 is the first to grow (Ginn and Melville 1983). Molting of rectrices is quite variable; however, the most frequent sequence is centrifuge, beginning in the central feathers (R1) and following a distal direction. These replacement patterns seem to be maintained in many passerines (Newton 1966, Voelker 2000, Mallet-Rodrigues and Marinho 2001), whereas non-passerine species show other sequence patterns (Stresemann and Stresemann 1966, Rasmussen 1987, Herremans 2000), among which are included the synchronous replacement of all the remiges (Pyle 2006), in which all feathers are lost simultaneously, hindering flight and thermoregulation.

In recent years an important contribution has been made to the terminology and understanding of the general features of the molt process in some Neotropical resident birds (Gualllar et al. 2009, Wolfe et al. 2010). However, the literature available for Neotropical birds continues being scarce, which hinders understanding these processes in functional or evolutionary contexts, highlighting the necessity for research on this theme in the region, especially to allow for comparative studies. Consequently, the aim of this study was to determine the replacement sequence of flight feathers during a complete molt (*sensu* Pyle 1997a) in the Blue-black Grassquit (*Volatinia jacarina*) and the Gray Seedeater (*Sporophila intermedia*), two bird species associated to the secondary scrub of the tropical dry forest, and common in the upper Magdalena valley, to the north of Tolima, Colombia.

METHODS

The study was conducted between February 2011 and January 2012 in the Centro Universitario Regional del Norte at Universidad del Tolima, municipality of Armero-Guayabal, north of Tolima Department, Colombia (05°00'N, 74°54'W; 280 masl). The area is a tropical dry forest, with a mean temperature of 28 °C and precipitation of 1791 mm, distributed in a bimodal regime. Birds in secondary scrub were captured by using 10 mist nets (12 × 2.5 m, 36 mm mesh), between 06:00–17:00 h, during 3 days per month, ensuring a monthly effort of 150 net hours. Individuals of Blue-black Grassquit and Gray Seedeater were marked with a unique combination of coloured rings, processed and released by following standardized methodologies (NABC 2001). To determine the age class, the WRP system was followed (Wolfe et al. 2010), using the terminology by Humphrey and Parkes (1959) with modifications by Howell et al. (2003).

The description of the feather replacement sequence followed Rohwer (2008). All the flight feathers of each individual were classified as new, old, or in growth. Each flight feather in growth was described as a fraction of its total length (based on observations from museum skins), by using decimal values from 0.1–0.9. Missing feathers were described as 0.01, while for totally developed feathers, but with quill traces at base a code of 0.99 was used. With the data obtained molt matrices were elaborated and used to generate summary tables of molt per species. Each molt matrix facilitated the assignation of nodal feathers, terminal feathers and replacement direction. A nodal feather was identified as that from which a molt series is begun; hence, a terminal feather was that which marks the end of a molt series. According to Yuri and Rohwer (1997) and Rohwer (2008), a nodal feather may be recognized (1) for being surrounded by old feathers, (2) for being surrounded by feathers in growth that are shorter than the focal feather, and (3) for having a neighbour old feather on one side and on the other side a feather in growth that is shorter than the focal feather. Terminal feathers are defined in situations opposite the nodal feathers, and the replacement direction is only assigned between adjacent pairs of feathers in growth, or with a feather in growth beside a new or old feather. These criteria allowed defining three possibilities: proximal replacement (towards the body or the center of the rectrices), distal replacement (towards the end of the wing or tail), or ambiguous direction (directionality cannot be assigned because of two growing feathers of the same length).

With feather and direction information in matrices per species, molt summary tables were elaborated. These were constructed by tabulating the frequencies of the nodal and terminal feathers, as well as the frequency in which a proximal, distal, or ambiguous replacement direction was recorded. Summary tables allowed evaluating the existence of molt series in flight feathers and examining the replacement sequence. Finally, summary tables were iterated with two objectives: first, to detect the limits among molt series, and second, to reorganize the summary table to properly show the series from the data (Rohwer 2008). In this process, molt series (i.e., primaries, internal secondaries, external secondaries) are separated by a column of zeros in the iterated summary (see Rohwer and Wang 2010), which facilitates their identification (see Rohwer 2008, Renfrew et al. 2011, Silveira and Marini 2012).

To evaluate the significance of the feather replacement direction, based on the summarized tables, a Wilcoxon signed rank test was used considering statistically significant those values of $P < 0.05$. First, the direction of each molt series was verified by using the total of the proximal and distal directions available in the summary table. Thereafter, the replacement direction between each pair of feathers within each molt series was evaluated, using the proximal and distal directions recorded on the principal matrix. Sample size did not allowed evaluating differences in the replacement sequence between immature and adult feathers. Given that adding data of immature to adult birds did not affect the results data was combined to improve test significance. In spite of the high recapture rates (see *Results*), birds going through the same molt process were around 1%; therefore these data were treated as independent and were combined with all others.

RESULTS

After a total sampling effort of 1800 net hours, 179 individuals of the two studied species were captured, with 94 individuals for the Blue-black Grassquit (5.2 ind/100 net hours; 52 males, 39 females, 3 undetermined), and 85 individuals for the Gray Seedeater (4.7 ind/100 net hours; 39 males, 46 females). An 11% recapture rate was obtained for the Blue-black Grassquit (10 individuals) and 21% for the Gray Seedeater (18 individuals).

Of the total number of individuals of Blue-black Grassquit, 61 registered molt. Of these, 52% were birds in definite pre-basic molt, 33% were undergoing a pre-formative molt, 10% were in pre-alternate molt, and 5% were in a first pre-basic molt. As for the Gray Seedeater, 57 individuals were undergoing molt: 54% were in definite pre-basic molt, 42% in pre-formative molt, and 4% in pre-alternate molt.

Blue-black Grassquit

The replacement direction in the primary remiges of the Blue-black Grassquit was distal ($n = 77$, $Z = 7.63$, $P < 0.001$). P1 is the only nodal primary, from where the molt proceeds toward P9, with this being the only terminal primary, which supports the observation that the primaries constitute a single molt series (Table 1). All the directions between pairs of primaries (i.e., P1-P2 to P8-P9) were statistically significant (Table 2).

The secondary remiges were divided into two molt series (Table 1). The direction between S1–S6 secondaries is proximal ($n = 35$, $Z = 4.64$, $P < 0.001$). Although there was no adequate sample between S1-S2 ($n = 3$) and S2-S3 ($n = 4$), the only nodal feather was S1 and the rest of proximal directions between pairs of secondaries within this series were significant (Table 2). The second molt series comprised the more internal S9–S7 secondary remiges. The start of this series was S8, given that it was the only nodal feather recorded ($n = 6$), and the molt sequence proceeds simultaneously toward S9 (6 proximal cases and 1 distal case) and toward

Table 1. Count summary of the molt scores (above) and iteration of the raw summary data (below) for the primary and secondary feathers of Blue-black Grassquit (*Volatinia jacarina*) individuals from the upper Magdalena valley, Tolima, Colombia. Iteration adjusts the score around P1-S1 and S6-S7 to recognize that the wing quills are divided into three molt series (P1–P9, S1–S6, and S8 to S7 and S9). Series are identified by bold numbers (indicating the main direction of replacement) and separated by a column of zeros. N: nodal feather, ←: proximal direction, →: distal direction, ?: ambiguous direction, T: terminal feather, #: number of feathers growing.

	Secondaries																		Primaries																
	9		8		7		6		5		4		3		2		1	-	1		2		3		4		5		6		7		8		9
Count summary																																			
N	0		6		0		0		0		0		0		0		0		4		0		0		0		0		0		0		0		0
←		6		1		3		**10**		**11**		**6**		**4**		**3**		9		0		0		0		0		0		0		0		0	
→		1		9		13		1		0		0		0		0		0		**8**		**10**		**10**		**13**		**9**		**10**		**8**		**9**	
?		1		1		0		1		0		0		0		0		0		0		0		0		0		0		0		1		0	
T	7		2		3		9		1		0		0		0		0		0		0		0		0		0		0		0		0		9
#	6		8		7		10		11		4		4		2		3		6		7		10		7		6		6		6		9		9
Iterated summary																																			
N	0		6		0		0		0		0		0		0		9		4		0		0		0		0		0		0		0		0
←		**6**		1		**0**		**10**		**11**		**6**		**4**		**3**		**0**		0		0		0		0		0		0		0		0	
→		1		**9**		**0**		1		0		0		0		0		**0**		**8**		**10**		**10**		**13**		**9**		**10**		**8**		**9**	
?		1		1		**0**		1		0		0		0		0		**0**		0		0		0		0		0		0		1		0	
T	5		2		16		12		1		0		0		0		0		0		0		0		0		0		0		0		0		9
#	6		8		7		10		11		4		4		2		3		6		7		10		7		6		6		6		9		9

S7 (9 distal cases and 1 proximal case). Additionally, S9 and S7 were terminal feathers in 7 and 3 occasions, respectively.

Evidence to support the existence of a second molt series among secondary feathers was found based on registering S7 as the terminal feather of the series on 3 occasions, without development in S6 or with this feather completely grown. S6 was annotated on 9 opportunities as a terminal feather, without growth in S7, or with series S9–S7 totally new. Additionally, the distal direction observed between S7-S6 is the result of S7 growing without development of S6, data that can be reorganized in the table of iterated data which permits clearly observing the presence of two independent molt series in the secondary feathers (Table 1).

Rectrices correspond to a single molt series, where R1 was frequently recorded as a nodal feather ($n = 9$), and R6 was terminal ($n = 9$) (Table 3). The replacement sequence is more strongly distal than proximal ($n = 42, Z = 3.04, P = 0.002$). R3 and R6 were annotated as nodal (on 1 occasion each), and R1, R2, and R4 as terminal feathers (on 2, 1, and 2 occasions, respectively); however these replacements are unusual and, despite suggesting the existence of more than one molt series among rectrices,

Table 2. Results of the Wilcoxon signed rank test for the replacement direction between pairs of flight feathers in Blue-black Grassquit (*Volatinia jacarina*) individuals from the upper Magdalena valley, Tolima, Colombia.

Pair	Direction	*n*	*Z*	*P*
P1-P2	Distal	8	2.388	0.0169
P2-P3	Distal	10	2.821	0.0048
P3-P4	Distal	10	2.829	0.0047
P4-P5	Distal	13	3.205	0.0013
P5-P6	Distal	9	2.675	0.0075
P6-P7	Distal	10	2.814	0.0049
P7-P8	Distal	9	2.539	0.0111
P8-P9	Distal	9	2.701	0.0069
S1-S2	Proximal	3	1.613	0.1025
S2-S3	Proximal	4	1.841	0.0656
S3-S4	Proximal	6	2.000	0.0264
S4-S5	Proximal	11	2.979	0.0029
S5-S6	Proximal	12	2.172	0.0299
S6-S7	-	16	2.389	0.0169 [a]
S7-S8	Distal	10	2.301	0.0214
S8-S9	Proximal	7	1.364	0.1724
R1-R2	Distal	10	1.998	0.0457
R2-R3	Distal	6	0.957	0.3387
R3-R4	Distal	10	1.958	0.0502
R4-R5	Distal	5	0.136	0.8923
R5-R6	Distal	11	2.150	0.0316

[a] A significative *P* value is result of being the limit between secondary molt series.

sample size of the replacement between pairs of feathers does not allow evaluating it in statistical terms. Also, in this molt series a high number of ambiguous directions ($n = 28$) was observed, concentrated between R2-R3 and R4-R5, which is why replacement in these pairs of feathers was not statistically significant in distal direction (Table 2).

Table 3. Count summary of the molt scores for the rectrices of Blue-black Grassquit (*Volatinia jacarina*) individuals from the upper Magdalena valley, Tolima, Colombia. Tail feathers represent a single molt series (R1–R6). Series are identified by bold numbers (indicating the main direction of replacement). N: nodal feather, ←: proximal direction, →: distal direction, ?: ambiguous direction, T: terminal feather, #: number of feathers growing.

	Rectrices										
	1		2		3		4		5		6
N	9		0		1		0		0		1
←		1		1		1		2		1	
→		**9**		**5**		**9**		**3**		**10**	
?		4		6		4		10		4	
T	2		1		0		2		0		9
#	7		12		12		14		13		14

Gray Seedeater

The replacement direction in the primary remiges of the Gray Seedeater was distal ($n = 70$, $Z = 7.36$, $P < 0.001$). P1 is the only nodal primary, from where the molt proceeds toward P9, which was exclusively a terminal feather (Table 4). All the directions between pairs of primaries (i.e., P1-P2 to P8-P9) were statistically significant (Table 5), indicating that the primaries constitute a single molt series.

In the secondary remiges two molt series were identified (Table 4). On the one hand, S1 is the nodal feather of the first series from where the replacement proceeds in proximal direction toward S5 ($n = 37$, $Z = 5.34$, $P < 0.001$); additionally, all the directions between pairs of secondaries within this series (S1-S2 to S4-S5) were statistically significant (Table 5). The second molt series comprised the most internal S9–S6 secondary remiges. The start of this series was S8, from where the molt proceeds simultaneously toward S6 ($n = 20$, $Z = 3.67$, $P < 0.001$) and toward S9 (4 proximal cases and 1 distal cases). Also S6 and S9 were found as terminal feathers in 9 and 3 occasions, respectively.

Secondary S5 was recorded on 7 opportunities as terminal feather, having previously

Table 4. Count summary of the molt scores (above) and iteration of the raw summary data (below) for the primary and secondary feathers of Gray Seedeater (*Sporophila intermedia*) individuals from the upper Magdalena valley, Tolima, Colombia. Iteration adjusts the score around P1-S1 and S5-S6 to recognize that the wing quills are divided into three molt series (P1–P9, S1–S5, and S8 to S6 and S9). Series are identified by bold numbers (indicating the main direction of replacement) and separated by a column of zeros. N: nodal feather, ←: proximal direction, →: distal direction, ?: ambiguous direction, T: terminal feather, #: number of feathers growing.

	Secondaries																		Primaries																
	9		8		7		6		5		4		3		2		1	-	1		2		3		4		5		6		7		8		9
Count summary																																			
N	1		1		0		0		0		0		0		0		0		6		0		0		0		0		0		0		0		0
←		4		1		0		0		**8**		**10**		**7**		**11**		**11**		0		0		0		0		0		0		0		0	
→		**1**		**8**		**11**		**9**		**1**		0		0		0		0		**6**		**7**		**9**		**11**		**8**		**5**		**10**		**14**	
?		0		0		1		0		0		0		0		0		0		0		0		0		0		0		0		0		0	
T	3		0		0		0		7		2		0		0		0		0		0		0		0		0		0		0		0		12
#	5		2		7		7		7		8		4		7		5		6		4		4		7		7		5		4		8		12
Iterated summary																																			
N	1		1		0		0		0		0		0		0		11		6		0		0		0		0		0		0		0		0
←		4		1		0		**0**		**8**		**10**		**7**		**11**		**0**		0		0		0		0		0		0		0		0	
→		**1**		**8**		**11**		**0**		1		0		0		0		**0**		**6**		**7**		**9**		**11**		**8**		**5**		**10**		**14**	
?		0		0		1		**0**		0		0		0		0		**0**		0		0		0		0		0		0		0		0	
T	3		0		0		9		7		2		0		0		0		0		0		0		0		0		0		0		0		12
#	5		2		7		7		7		8		4		7		5		6		4		4		7		7		5		4		8		12

Table 5. Results of the Wilcoxon signed rank test for the replacement direction between pairs of flight feathers in Gray Seedeater (*Sporophila intermedia*) individuals from the upper Magdalena valley, Tolima, Colombia.

Pair	Direction	*n*	*Z*	*P*
P1-P2	Distal	6	2.226	0.0260
P2-P3	Distal	7	2.384	0.0171
P3-P4	Distal	9	2.680	0.0074
P4-P5	Distal	11	2.950	0.0032
P5-P6	Distal	8	2.588	0.0096
P6-P7	Distal	5	2.041	0.0412
P7-P8	Distal	10	2.970	0.0030
P8-P9	Distal	14	3.341	0.0008
S1-S2	Proximal	11	2.947	0.0032
S2-S3	Proximal	7	2.388	0.0169
S3-S4	Proximal	10	2.825	0.0047
S4-S5	Proximal	9	2.807	0.0050
S5-S6	-	8	2.546	0.0109 [a]
S6-S7	Distal	11	2.956	0.0031
S7-S8	Distal	9	2.079	0.0376
S8-S9	Proximal	5	1.511	0.1308
R1-R2	Distal	6	2.226	0.0260
R2-R3	Distal	7	1.194	0.2325
R3-R4	Distal	6	2.232	0.0256
R4-R5	Distal	8	1.420	0.1557
R5-R6	Distal	8	2.539	0.0111

[a] A significative *P* value is result of being the limit between secondary molt series.

Table 6. Count summary of the molt scores for the rectrices of Gray Seedeater (*Sporophila intermedia*) individuals from the upper Magdalena valley, Tolima, Colombia. Tail feathers represent a single molt series (R1–R6). Series are identified by bold numbers (indicating the main direction of replacement). N: nodal feather, ←: proximal direction, →: distal direction, ?: ambiguous direction, T: terminal feather, #: number of feathers growing.

	Rectrices										
	1		2		3		4		5		6
N	6		0		1		0		1		0
←		0		1		0		1		0	
→		**6**		**6**		**6**		**7**		**8**	
?		0		0		1		3		3	
T	0		1		1		1		3		11
#	4		6		6		7		11		10

ended the development of S6, which supports the existence of a second molt series among the secondaries. Additionally, the distal replacement direction found between S6-S5 is the result of the S6 growth registry without development of S5, which can be reorganized in the table of iterated data clearly showing the presence of both series (Table 4).

Rectrices correspond to a single molt series (Table 6). R1 was frequently recorded as a nodal feather ($n = 6$), while R6 was a terminal feather ($n = 11$), with the molt proceeding in distal direction ($n = 35$, $Z = 4.22$, $P < 0.001$). Upon revising the directions between pairs of rectrices, only 2 of them were not statistically significant, perhaps due to the effect of the sample size between R2-R3 (6 distal cases and 1 proximal case) and R4-R5 (7 distal cases and 1 proximal case) (Table 5). Additionally, rectrices R2 to R4 were annotated as terminal feathers in 1 occasion, and R5 on 3 opportunities. Also, some ambiguities were observed in the replacement direction between R3-R4, R4-R5 and R5-R6.

DISCUSSION

The summary tables of the molt obtained for the data of the Blue-black Grassquit and the Gray Seedeater allowed observing in detail the replacement sequence of flight feathers and the existence of various molt series within them. Although in both species combined data of adult and immature individuals were used, the proportion of records taken from birds in pre-formative molt was relatively low (23–28%) and did not affect the general molt pattern found in adults. For these two species, combined data of the mentioned age groups improved the significance of the signed test for some directions between pairs of feathers. However, whenever data permits, these analyses should be conducted discriminating by age classes (Rohwer and Wang 2010) to better define molt paterns based on plumage sequence.

The primary remiges of the Blue-black Grassquit and the Gray Seedeater constitute a single molt series, which proceeds according to the pattern observed in most passerines (Ginn and Melville 1983), from P1 in distal direction toward P9. Silveira and Marini (2012) proposed that because the more external primary feathers play the most important role in flight development (Jenni and Winkler 1994), and at the same time wear out more than the internal primary feathers (Langston and Rohwer 1995), the proximal–distal molt pattern of the primary feathers could be an adaptive response. In spite of this generalization, exceptions exist to the basic sequence (Pyle 1997b), which is why detailed studies are required to detect and evaluate the replacement order of flight feathers (Voelker 2000, Renfrew et al. 2011, Silveira and Marini 2012).

The ambiguous direction observed among the primaries of the Blue-black Grassquit corresponds to an individual molting P7–P9 simultaneously, where P7 and P8 were described with equal growth value; however, P9 showed lower development, suggesting that the ambiguous direction between P7-P8 was caused by the impossibility of correctly assigning the proportion of P7 growth. This difficulty, commonly found, could be avoided by measuring the length of completely developed feathers, thus calculating the length of missing feather and converting the data to fractions of the missing feather (Silveira and Marini 2012). However, doubt remains in cases where totally grown feathers have the same length and which present a tendency to grow simultaneously, as observed in some rectrices of the species in this study, which is why an increase in sample size could aid in defining and evaluating if the simultaneous development of two feathers could be considered a particular replacement strategy.

The secondary remiges are divided into two molt series in both species, according to the basic sequence described by Ginn and Melville (1983). It states that S9–S7 (tertiary feathers) tend to be molted before S1, so that the last feather to molt is generally S6 (Ginn and Melville 1983, Pyle 1997a). In the Blue-black Grassquit, the series of internal secondary feathers S9–S7 molt in the exact sequence described by Ginn and Melville (1983), with S8 being the first to grow and then the contiguous feathers. Recent studies have also found this pattern in Neotropical passerines (Renfrew et al. 2011, Silveira and Marini 2012). The secondary remiges of the Gray Seedeater show a different replacement sequence, which lies in that the internal series of secondary feathers, which begins in S8 (similar to that observed in the Blue-black Grassquit), molt in distal direction up to S6. Although Rohwer (2008) documented a similar case in *Tyrannus verticalis*, the explanation for this pattern is not clear. It could be related to the aerodynamic necessity to replace S6 prior to the molt of the external secondaries (Rohwer 2008). Nevertheless, this pattern could also be the consequence of the high variability observed in the molt of the tertiary remiges in Passeriformes (Ginn and Melville 1983).

Rectrices comprise a single molt series in both species, which advances in centrifuge direction from R1. The existence of several nodal and terminal feathers within this series could be caused by unusual replacement of feathers, given that the rectrices are quite susceptible to detachments independent of the molt cycle (Pyle 1997a, Gualla et al. 2009) induced by the effect of predatory attempts, aggressive behaviors, or simply by friction against structures in the habitat (Pyle 1997a). Nonetheless, the amount of ambiguous directions recorded suggests that, on occasions, simultaneous growth occurs of certain pairs of feathers or even of the totality of the rectrices, a case found in 12% of the birds (4 individuals) and which has also been found in other passerines (Ginn and Melville 1983).

The Blue-black Grassquit and the Gray Seedeater are considered closely related species (Remsen et al. 2014), which besides coexisting in great part of its distribution (Restall et al. 2006) share similar habits and diets (Hilty and Brown 1986). In spite of these similarities, the replacement sequence of secondary remiges was different among them. Given the high energetic demands of molting, it might be possible that similar species may evolve different mechanisms to carry on this event. This would also support a high phenotypical plasticity among and within lineages to allow for fine-tuning in terms of regulation and molt sequence. Given current global changes, this would certainly be a topic in which to explore further, looking at the possibilities for fast adaptation.

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