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Primary molt in *Psophia* and simpler molt summary tables

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Abstract. Molt summary tables reveal the sequence and mode of flight feather replacement and how these feathers are divided into independent replacement series. These tables are relatively new, and the first illustration for generating molt summary tables used a temperate passerine. But primary replacement in temperate passerines is far too simple to address the complexities of generating summary tables for: (i) species with primaries divided into more than one replacement series, (ii) species with stepwise primary replacement, (iii) species that do not replace all their flight feathers annually, and (iv) species for which flight feather replacement has been studied for the entire wing. Here, we review complications that arise in the development of molt summary tables and offer solutions that remove ambiguity both in the direction that molt proceeds through the wing and in the recognition of nodal and terminal feathers, which start and stop waves of feather replacement. We use these modified molt summary tables to describe the sequence of primary replacement in trumpeters, a group for which primary replacement is reported to be reverse that of most other birds, but for which there has never been a detailed study of primary replacement. Using the 80 specimens of *Psophia crepitans* at the American Museum of Natural History, we develop molt tables that show that the sequence of primary replacement is, indeed, proximal. Further, summary tables reveal that *Psophia crepitans* has its primaries divided into two replacement series, one beginning at outermost primary P10, and the other beginning at P3. One juvenile confirms these primaries as the beginning of the two replacement series in the wing of *Psophia crepitans*.

Keywords: flight feather molt, molt tables, production of independent young, *Psophia crepitans*, trumpeters

INTRODUCTION

Most studies of replacement patterns in the flight feathers of birds rely on “snap-shot” data assembled across many individuals for which the age and growth of flight feathers was recorded just once. In the past 20 years the use of molt summary tables has revealed previously unsuspected complexities in the patterns of primary and rectrix replacement in several groups of birds. Langston and Rohwer (1995), who first developed these tables, showed that two species of North Pacific albatrosses have divided their primaries into two replacement series that are replaced in opposite directions. Shugart and Rohwer (1996) showed that the primaries of night herons constituted a single replacement series, but that the mode of replacement in adults was stepwise, with up to four waves proceeding simultaneously through the 10 primaries. Silveria and Marini (2012) showed the primaries of a puffbird to be divided into two molt series, and two swallows and a kingbird have now been documented to have their outermost rectrix, R6, replaced as a unique series independent of the timing of molt completion for the other five rectrices (Yuri & Rohwer, 1997; Imlay et al., 2017; Rohwer, 2008). These recent discoveries have been facilitated by the use of molt summary tables, which are particularly valuable because they reveal the adequacy of the data used to deduce the rules of flight feather replacement. Nowhere is this more important than for species with less intuitive molt sequences, whose primary replacement has been described as chaotic, complex, random, or transilient (Stresemann & Stresemann, 1961; Siegfried, 1971; Ginn, Glue & Hawthorn, 1974; Hamner, 1995; Herremans, 2000). Given the importance of flight feathers, and the temporal and physiological costs of molt, and the need to replace feathers every one to two, or sometimes, three years, it is hard to imagine that selection on such an important life-history event would be haphazard.

A primary lesson from the past 20 years of more quantitative studies of flight-feather replacement is that replacement rules were often not being correctly inferred for groups with complex patterns of replacement, and that there is great diversity among birds, not only in how their flight feathers are organized into replacement series, but also in how frequently feathers are replaced in those series, and in the direction and mode of replacement in those series. Simple, distal replacement of the primaries is the rule in many groups of birds, but distal replacement is often stepwise in large birds, wherein a variable number of waves of replacement proceed simultaneously through the primaries (Howell, 2000). In other groups the primaries are divided into multiple replacement series, and some have joined the inner primaries with the outer secondaries into a single replacement series. Moreover, a few species are reported to have switched the directionality of the primary molt, wherein molt begins at the outer most primary and proceeds toward the body. On the basis of just six specimens, the trumpeters were reported by Stresemann and Stresemann (1966) to replace their primaries proximally, toward the body, unlike most other species. Here, we provide the first detailed examination of primary molt in the Grey-winged Trumpeter (*Psophia crepitans*), and use data from this species to illustrate simpler molt summary tables.

Inferring the direction of replacement in the primaries can be difficult for many tropical birds that seldom have more than a single primary growing per wave of feather renewal. Thus, with an aim of simplifying the procedures proposed by Rohwer (2008) for determining the rules of flight feather replacement, we divide the results of this paper into two sections. The first is a set of comments on the best methods for casting raw molt scores into summary tables designed to reveal and communicate the rules of flight-feather replacement. We illustrate the suggested improvements for creating molt summary tables using our data on Grey-winged Trumpeters, and further illustrate common pitfalls and problems in interpreting summary tables with a variety of recently published studies. Second, we use these same tables to show that the primaries of *Psophia* are, not only replaced proximally, but that they are also divided into two replacement series, both with proximal replacement. Further, replacement in the outer primary series is sometimes stepwise, with two or three waves of replacement separated by older feathers proceeding simultaneously through the outer primaries.

NATURAL HISTORY AND MOLT SCORING

Trumpeters are a family of forest birds endemic to South America and restricted to lowland regions of Amazonia and the Guiana Shield. They remain common where forests are intact but have declined greatly with forest clearing in many parts of their previous range. They are rotund, chicken-sized birds with long necks and legs, and are reluctant to fly. They often live in large groups and lay 2-5 eggs in tree hollows; multiple males help raise the precocious young produced by the dominant female of the group (Sherman & Bonan, 2018). Trumpeters are often kept as pets or watch dogs both because of their proclivity to give loud trumpeting calls in response to threats and because of their reputation for killing snakes. As is characteristic of many highly social animals, they are easily tamed and regularly raised from chicks (Sherman & Bonan, 2018). These tame birds would be ideal for further documenting patterns of secondary replacement, which we could not score for molt using the traditional study skins available in museums. Because they are forest birds, the primaries fade little between molts, so scoring feather age was largely based on feather wear.

Growing primaries were scored as decimal fractions of their full length. Because trumpeters have short rounded wings and seldom have adjacent primaries growing at the same time, these decimal fractions were sufficient for inferring replacement direction between adjacent pairs of growing feathers. Feathers we judged to have been recently replaced were scored as 1 for new, while feathers judged to have been replaced in a previous episode of molting were scored as 0 for old. Because trumpeters are forest birds that seldom fly and, thus, show little fading of feather color, birds with feathers of ambiguous age were scored as 0/1 to indicate that we were uncertain if they were new or old. In all cases where we had growing feathers to compare with full length feathers, the color and wear status of fully grown feathers was compared to that of the growing feathers to assure as much accuracy as possible in assigning feather ages.

All of the fully-grown birds scored for molt were aged as juveniles or adults on the basis of the width and shape of the rectrices. Juvenile rectrices are narrower and more pointed than those of adults (S. Rohwer & V. Rohwer pers. obs., 2018). For age determination we carefully examined all the rectrices, as some juveniles were in the process of replacing their tail feathers. There was no ambiguity about birds that were fully grown, and we found just a single downy chick among the 80 fully grown *Psophia crepitans* in the American Museum of Natural History (AMNH) collection.

RESULTS

A sequential approach to documenting replacement series and replacement direction.

Molt summary tables are valuable because they reveal the sample of growing feathers available at every feather locus for inferring the rules of feather replacement. For this reason, the first generation of these tables emphasized counts of growing feathers (Langston &

Rohwer, 1995; Shugart & Rohwer, 1996; Yuri & Rohwer, 1997; Filardi & Rohwer, 2001). In all these early tables, the direction of replacement for a growing feather was scored by the state of its neighboring feathers. This generated ambiguous scores for direction at all nodal feathers with two neighbors that were old, and for all terminal feathers when both neighbors were new or less than full grown. Such scores of ambiguous direction are uninformative because they are always associated with feathers that scored either as nodal or terminal. Further, scoring direction by the state of a focal feather's two neighbors was confusing because direction is intuitively understood to be inferred between adjacent feather pairs. Rohwer (2008) attempted to better formalize the development of molt summary tables, primarily by recognizing that directionality scores belonged between adjacent primaries, involving at least one growing feather. However, Rohwer (2008) advocated scoring direction of replacement at the same time that feathers were assigned nodal or terminal status. This works fine is species with complete molts but generates many contradictions in replacement direction in species with incomplete molts (e.g. Shugart & Rohwer, 1996) and in species with multiple waves of feather replacement (e.g. Rohwer & Broms, 2013). Thus, we suggest here that the first summary table should 1) summarize nodal and terminal feathers, and 2) assign direction *only* between feather pairs for which neither is nodal or terminal. This sequence of scoring and of creating summary tables avoids the ambiguities of direction caused by transient nodal and terminal feathers that occurred under the first generation of summary methods. The advantage of this summary method is well illustrated in the molt tables we present here for *Psophia*.

Unfortunately, Rohwer's (2008) example for the generation of molt summary tables fails to deal with a variety of complications that emerge as these tables are applied to species with complex or incomplete flight feather replacement. Here we review these complications with reference to papers that have resolved these issues effectively.

Nodal feathers. Nodal feathers are highly informative because they generally mark the beginning of a molt series. However, there are stable (or dominant nodes), and transient nodes, which are distinguishable using summary tables (see below). Stable nodes mark the first feather in a replacement series. In contrast, transient nodes mark sites where molt was reinitiated following an arrest in molt. For a transient node to qualify as nodal, the arrest was probably of long duration because long arrests are required for the upstream neighbor to have had sufficient use to score as old. But, feather age is difficult to assign in species that show little wear or foxing between molt cycles, like forest dwelling trumpeters that seldom fly. Feather ages may also be difficult to assign in species that replace limited numbers of flight feathers in more than one bout of molting per year. For example, some raptors replace feathers before and after breeding (e.g. Prevost, 1983; Edelstam, 1984), and this would make feather generations difficult to distinguish in forest raptors that undergo two bouts of incomplete flight feather molt annually.

Terminal feathers. Feathers that score as terminal are of little help in deducing the rules of flight feather replacement because feathers that actually mark the end of a flight feather series rarely score as terminal when replacement is complex. The obvious exception is the outer-most primary in passerines. Because almost all passerines replace their primaries from P1 to P9 or 10 and have complete molts, the outermost primary will be the last to growth and, thus will score as terminal. However, when replacement direction converges on two internal terminal feathers, only the last of the two terminals to be replaced will score as terminal; the other must be inferred to mark the end of its molt series by direction of replacement and the adjacent terminal feather in the other series (a difficult case of this is illustrated for the inner two replacement series in albatrosses (Edwards & Rohwer, 2005). When the flight feathers are broken into multiple replacement series and molt proceeds more or less synchronously and in the same direction, terminal feathers that mark the end of a series will legitimately be recognized by having newer neighbors, as was the case in cuckoos (Rohwer & Broms, 2013). However, such internal terminal feathers would not score terminal if molt finished in one series before it started in the adjacent series. There is, as yet, no clear illustration of this problem. Despite these problems, growing feathers flanked by newer feathers should be scored as terminal because this then identifies them as feathers that should not be used in preliminary directional scoring (see next paragraph).

Nodes and contradictory direction. Direction of replacement should never be scored for feathers that score as nodal or terminal. The reason is that every nodal or terminal feather with two neighbors will generate contradictory directionality scores that fail to help reveal the direction molt proceeds in a replacement series. Thus, direction should never be scored between transient nodal or terminal feathers and their neighbors, and direction should be scored for stable nodes and for feathers that mark the end of molt series *only* after those feathers have been clearly recognized as such.

Most stable nodes are recognized by their high frequency, compared to transient nodes associated with arrests, which are scattered throughout a replacement series (e.g. Rohwer & Wang, 2010; *Psophia*, this paper; Shugart & Rohwer, 1996). It is important to realize, however, that stable nodes cannot be recognized by frequency alone when the frequency of feather replacement varies across the wing. For example, North Pacific albatrosses replace their outer three primaries annually, but they replace the two inner feathers of the outer primary series and their inner primaries and middle secondaries only every two or three years (Langston & Rohwer, 1995; Edwards & Rohwer, 2005). Thus, stable nodes could only be recognized in these feather groups by computing the probability of a feather being nodal based on how frequently it was replaced in birds that had recently completed their molt. When this was done, the stable nodes became readily apparent at P6, P5, and S5, with each marking the beginning of a separate replacement series (Edwards & Rohwer, 2005).

Stepwise molters make the generation of molt tables relatively easy because, after the first wave of replacement has reached the outermost primary, stepwise molters tend to replace all their primaries at about equal frequencies. (Stepwise replacement is largely unstudied in secondaries, but occurs in some of the secondary series in North Pacific albatrosses: Edwards & Rohwer, 2005) When the primaries are all replaced at about equal frequency, stable nodes will be far more common than transient nodes. But some species with multiple replacement series in the flight feathers vary the rate of replacement of feathers across series. When this is the case, stable nodes must be identified by rates rather than high frequencies, because rates correct for differences in the frequency that feathers in different parts of the wing are replaced (Edwards & Rohwer, 2005).

Morphology does not define series boundaries. It is essential to appreciate that inner primaries and outer secondaries may be combined into a single replacement series, as occurs in Falcons, Parrots, and North Pacific albatrosses (Miller, 1941; Pyle, 2005; Pyle, 2013; Edwards & Rohwer, 2005). Thus, primaries growing in two separate places do not necessarily imply that replacement of the primaries is stepwise. Instead, the primaries may be broken into more than one molt series, which Howell (2006) failed to recognize for North Pacific albatrosses (Rohwer & Edwards, 2006). This is best illustrated in cuckoos, where the primaries are broken into 3 or 4 replacement series, a point that previous molt studies of cuckoos had failed to discover because efforts to summarize their molt assumed the primaries were a single series and attempted to define the sequence of replacement as a single series. But this fails to reveal patterns if the series are not divided into equal lengths of feather and if the series fail to initiate molt simultaneously (Rohwer & Broms, 2013).

This caveat means that, if possible, all flight feathers of the wing should be scored for molt. Unfortunately, scoring secondaries is extremely difficult on large birds that were prepared as traditional study skins. For this reason, we strongly encourage those preserving avian specimens to remove at least one wing from round skins or skeletons and preserve that wing, fully extended, as a separate specimen. Extended wings offer three great benefits to studies of flight feather replacement. First, they make it possible *and* easy to score secondary molt. They also make it easy to account for the fact that the number of secondaries may vary substantially among individuals in species of large birds with long wings, such as albatrosses (Edwards & Rohwer, 2005). Without preserved extended wings or without being able to examine living birds whose wings can be fully extended, molt scores simply cannot be assigned for the secondaries of most large birds. Second, extended wings greatly facilitate measuring the lengths of the flight feathers. Finally, growth bands can be measured in the feathers of extended wings, which, especially when growth bands are faint, is impossible on traditional study skins (e.g. Rohwer & Broms, 2013). These last two measures are essential for calculating the number of days required to replace the feathers of a replacement series (Rohwer & Broms, 2013; 2012).

Primary replacement in *Psophia crepitans*

Our raw data represents the molt status of the 74 adult *Psophia crepitans* available in the collection of the AMNH. Data for all 80 specimens, including the 6 juveniles, is posted as a supplemental data file (Data S1). All of the AMNH specimens were old round skins and trumpeters are too large for secondary molt to be scored without substantial damage to specimens. Thus, there is a great need to save extended wings from future specimens. Because trumpeters are often kept as pets or watchdogs, the best opportunity to document the replacement rules for their secondaries may be to score flight feather molt multiple times on tame individuals associated with farms or villages that can be recaptured.

We developed the molt summary tables for the raw data in two steps, as proposed above. First, for adults, we recorded and counted all nodal and terminal feathers in the raw data, and assigned directionality score only between feather pairs that included neither nodal or terminal feathers (Table 1). This table clearly reveals two dominant nodes in the primaries, marking the first feather in their molt series. P10 was nodal in 12 specimens and P3 was nodal in 9 specimens. In contrast, feathers between P9 and P4 scored as nodal from 0 to 2 times, suggesting that these were transient nodes associated with the re-initiation of molt following arrests. P3 scored as nodal 9 times, but this frequency can only be compared to that for P2, which has two scored neighbors. P2 received 3 nodal scores and 2 terminal scores, and these low nodal scores compared to P3, suggest P3 is first feather of a replacement series that includes the inner primaries. The observation of 6 nodal scores associated with P1 is addressed below.

The leap from Table 1 to Table 2 is short, involving just three steps. First, because directionality between all feather pairs between P9 and P4 was strongly proximal, it is appropriate to add directionality scores between P10 and P9, which are proximal in 7 cases and distal in 3. It might seem that the three distal scores suggest problems of interpretation, but P10 is rather short compared to P9. Thus, P10 may sometimes complete growth before P9, even when P9 is lost after P10, because P9 takes longer to grow. Second, directionality scores between molt series should be dropped (see above and Rohwer, 2008). This eliminates the two cases of proximal directionality between P4 and P3; in both cases P4 was growing and P3 was old. A grey bar can now be added between P4 and P3 to identify the boundary between the outer and inner replacement series in the primaries, and the two proximal scores between P4 and P3 can be inferred as terminal scores for P4, increasing the terminal counts for P4 from 2 to 4. Third, with P4 established as terminal in the outer replacement series, it is now appropriate to assign replacement direction between P3 and P2; these scores are proximal in 9 out of 9 cases. Note that these directionality scores would have all been contradicted by scores of distal between P3 and P4, had they been applied before establishing that P4 was the terminal feather in the outer primary molt series. Samples of adult *Psophias* molting the inner most primaries are small, so our inference of proximal directionality between P2 and P1 is weak. The directionality scores between P3 and P2 are strongly proximal, suggesting directionality between P2 and P1 should be similar; indeed, in one juvenile (AMNH 125285), directionality between P2 and P1 is proximal.

There were just 6 juveniles among the 80 specimens of *Psophia crepitans* in the AMNH collection. One of these juveniles, AMNH 125285, was initiating molt at P10 and P3, thus confirming that these feathers mark the start of the two replacement series in the primaries. AMNH 431790 fails to confirm the series we identified using adults, but we probably erroneously aged P3 through P1 as juvenile feathers. Recall that feather ages were difficult to assign because they show little wear or fading; thus, in the case of birds aged as juveniles, we tended to record feathers that appeared to be old as j (juvenile), rather than 0 (old) or 1 (new).

Why does P1 frequently receive nodal scores? In reality these nodal scores are inappropriate if the inner primaries and the outer secondaries are part of a single replacement series. Unfortunately, we could not score secondary replacement in the round skins at the AMNH, but we suspect the inner primary molt series will extend into the secondaries, as it does in falcons, parrots and, at least, two albatrosses (references above). Further, our data support this supposition because all six cases of P1 scoring as nodal were because P2 was old and P1 was new or growing. In three of those six cases P1 was new, suggesting that S1 may also have been new or growing. If those 3 nodal scores for P1 were eliminated, the suggestion that other nodal assignments for P1 were all transient nodes associated with molt arrests seems plausible. However, without secondary scores this is purely speculative.

Primary replacement is stepwise in the outer series

The primaries from P10 to P4 are a single molt series replaced proximally. Those between P9 and P4 received scores of nodal or terminal from 0-3 times. The regular occurrence of transient nodal and terminal feathers between P9 and P4 strongly suggests that primary replacement in *Psophia's* outer replacement series is stepwise and, further, that molt is regularly interrupted and restarted, both where it was arrested and also at P10. A consequence of stepwise primary replacement is that all feathers of stepwise replacement series are eventually replaced at approximately equal frequencies. It is important to realize that this mode of replacement is the reason that stable nodes can be identified by frequency alone, without having to adjust for rate differences in replacement to find stable nodes, as was necessary in albatrosses (Edwards & Rohwer, 2005).

From studies of a very limited number of juveniles of 13 species of large birds undergoing their first replacement of primaries, we know that, in birds that feature stepwise primary replacement, multiple waves of replacement develop following molt arrests (Rohwer, 1999). Thus, after each arrest, molt is reinitiated where it stopped in the first (or later) bout(s) of molting, and also at the first primary in the molt series. In the case of *Psophia* with its unusual proximal direction of replacement, these new waves would start at P10.

In the outer primary molt series, which was fully assessed, 74 adults were scored for active molt. 36 were not growing primaries, while 38 were growing one or more primaries in the outer series (Table 3). Of the 38 growing primaries, 31 had just a single wave of replacement, but 6 had 2 waves and 1 had three waves of replacement, showing that molt is often reverse stepwise in *Psophia's* outer primary series. In the inner primary series, which likely includes an unknown number of secondaries that could not be assessed, none of the 18 birds replacing feathers between P3 and P1 had more than a single wave of replacement. Note that, with just three feathers scored in this series, the likelihood of recording two waves so close together is very small, especially with just 18 birds showing active molt in these feathers.

The case for stepwise replacement in the outer primaries is further supported by patterns of old and new feathers in that series. Of the 36 adults that were not growing primaries in the outer series, 26% had mixes of old and new feathers that demonstrated molt arrests. This percent closely matches the 23% of specimens in active molt that were replacing their primaries in two or three waves. Most of the 36 specimens that were not in active molt had single waves of newish feathers that abutted or lay between blocks of old feathers, but at least one showed evidence of molt arrests involving more than a single replacement wave.

Production seems very low in Psophia.

There were 80 fully grown specimens of *Psophia crepitans* in the collection at the AMNH, all of which we aged by rectrix shape. We were surprised to find just 6 birds in this collection with either all juvenile rectrices (n = 1) or a mix of juvenile and adult rectrices (n = 5). Because juveniles closely resemble adults in appearance and because we could only age these collected specimens with reference to rectrix shape, it seems unlikely that collectors were preferentially targeting one of the other of these age classes. Thus, production of what we assume are independent young seems to be very low in *Psophia crepitans*, at about 0.075 juveniles per adult per year. *Psophia* live in groups, with several males assisting in rearing the chicks produced by a single female, so some of the adults we examined were surely not breeders. Nonetheless, this seems like a very low rate of production, suggesting that mature birds are long-lived. Unfortunately, we do not know how long juvenile rectrices are retained in these birds; if they are replaced by adult rectrices before young are a year of age, then our estimate of production would be low.

DISCUSSION

We accomplish two things in this paper. First, we refine earlier methods for developing molt summary tables that clearly show the data and reasoning behind inferences about modes of flight feather replacement. For many small temperate passerines with intense primary molts, molt tables may seem to be unnecessarily complicated. However, they do reveal the adequacy of the data for making inferences about molt series and replacement direction within series.

Further, in a kingbird and two species of swallows, the use of molt summary tables has revealed that the outermost rectrix is replaced on a schedule that precludes it being part of the R1-5 series (Yuri & Rohwer, 1997; Rohwer, 2008; Imlay et al., 2017). For many birds with more complex patterns of flight feather replacement, summary tables are essential for uncovering complexities that otherwise have gone unnoticed. This is well illustrated for albatrosses (Langston & Rohwer, 1995; Edwards & Rohwer, 2005), night herons (Shugart & Rohwer, 1996), a tree swift (Rohwer & Wang, 2010), and cuckoos (Rohwer & Broms, 2013). We use those studies and others to summarize some of the caveats that need to be considered in transcribing raw molt scores into summary tables. In this paper, our principle contribution to that process is to show that direction of replacement should not be scored between feathers that score as nodal or terminal and their neighbors, simply because directionality scores are uninformative for nodal and terminal feathers with two neighbors.

Our second finding in this paper confirms that *Psophia* replace their primaries proximally, from outermost P10 to P1 (Stesemann & Stresemann, 1966). Molt summary tables also revealed that *Psophia* primaries are divided into two replacement series, one being P10-P4, and the other starting at P3, and likely including some outer secondaries. This was a surprise and may be an adaptation either to allow more rapid renewal of the flight feathers, as occurs in cuckoos (Rohwer & Broms, 2013), or the division into two series could be an adaptation that allows feathers in the middle of the wing to be replaced less often than feathers at the tip of the wing that suffer more wear, as occurs in some albatrosses, where middle molt series are not activated every year (Langston & Rohwer, 1996; Edwards & Rohwer, 2005).

So far as we know proximal replacement of the outer primaries or of the whole primary series has been reported in only three groups of birds, Limpkins, *Aramus guarauna*, (Stressemann & Stressemann, 1966), *Psophia* (this paper), and the Spotted Flycatcher, *Muscicapa striata*, of Eurasia (Williamson, 1972). Of these three sets of birds, only *Psophia* has been reported with quantitative tables, so we cannot know whether or not Limpkins and Spotted Flycatchers have their primaries organized as a single molt series that is simply replaced inward, or whether they may also have their primaries organized into more than a single molt series, with an inner series that may include some outer secondaries. Why should primary replacement proceed proximally in these three groups of birds, when it proceeds distally in most other birds? For Limpkins, Howell (2010) has suggested proximal replacement could facilitate early replacement of P10, which is sickle-shaped in adults and may be used in display. Alternatively, both limpkins and *Psophia* live in rather dense vegetation where flight may damage outer primaries more than the middle wing feathers. If that were the case, then selection could favor renewing the outer primaries first. Note, however, that both suggestions should apply to many other groups of birds, making them seem implausible. Unless more groups are discovered in which the outer primaries are replaced proximally, there seems little chance that proximal and distal replacement of the primaries can be associated with potential selective regimes. Perhaps more likely is that their unusual replacement direction has arisen from some accidental gene inversion, which has generated proximal replacement and drifted to fixation because the direction of primary replacement has little or no fitness consequences.

CONCLUSION

Primary replacement in *Psophia* appears to combine both multiple series and stepwise molt, a strategy that, to date, has not been recorded in any other species. This unexpected complexity in the pattern of primary replacement likely would have been overlooked without the use of molt summary tables. Yet, these seemingly subtle differences in molt strategies, like those observed in *Psophia*, represent important evolutionary transitions for organizing and scheduling the replacement of flight feathers, and provide a richer understanding of flight-feather replacement across species. As more such reports accumulate, the stage will be set for a comparative analysis of the transitions between modes of flight feather replacement across living birds.

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Table 1(on next page)

Table 1. First molt summary table for the primaries of 74 adult *Psophia crepitans*.

In this table all nodal and terminal feathers are counted, as are all directionality scores involving feather pairs where neither scored as nodal nor terminal. Note that nodal and terminal scores for P1 do not consider the status of S1, so may be in error.

Table 1

	P10		**P9**		**P8**		**P7**		**P6**		**P5**		**P4**		**P3**		**P2**		**P1**
# nodal	12		2		1		0		2		1		1		9		3		6
# p				11		8		6		7		3		2				0	
# d				0		0		1		0		1		0				0	
# terminal	3		1		1		0		1		3		2		0		2		3
# growing	6		11		8		3		8		7		5		7		4		6

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Table 2(on next page)

Table 2. Final molt summary table for the primaries of 74 *Psophia crepitans.*

In this table we have added directionality scores between nodal and adjacent feathers, removed the directionality scores between terminal P4 and nodal P3, and added a grey bar to mark the series break between P4 and P3.

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Table 2

	P10		**P9**		**P8**		**P7**		**P6**		**P5**		**P4**		**P3**		**P2**		**P1**
# nodal	12		2		1		0		2		1		1		9		3		6
# p		7		11		8		6		7		3				9		0	
# d		3		0		0		1		0		1				0		0	
# terminal	3		1		1		0		1		3		4		0		2		3
# growing	6		11		8		3		8		7		5		7		4		6

Table 3(on next page)

Table 3. Number of replacement waves and growing feathers in the 74 adults *Psophia crepitans.*

Table summarizes the number of replacement waves and growing feathers in the inner and outer molt series of the 74 adults we scored.

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Table 3

	Number of feathers growing per series				
	0	1	2	3	Totals
P10-4 series	36	31	6	1	74
P3-1 series	56	18	0	0	74