

EVOLUTIONARY IMPLICATIONS OF SYNAPOMORPHIC WING-MOLT SEQUENCES AMONG FALCONS (FALCONIFORMES) AND PARROTS (PSITTACIFORMES)

PETER PYLE¹

The Institute for Bird Populations, P.O. Box 1346, Point Reyes Station, CA 94956

Abstract. I examined over 4500 specimens to investigate the evolutionary significance of molt sequences as related to systematic relationships of falcons and parrots. Nodes of molt among the medial primaries (p4–p6) and at s5 among the secondaries, followed by bidirectional replacement from the node within each tract, was confirmed for most or all taxonomic groupings of both falcons and parrots, with the exception of the Kakapo or Owl Parrot (*Strigops habroptila*), which appears to replace its remiges in sequences similar to those of most other birds. Initiation of primary molt varies between p4 and p5 in falcons and between p5 and p6 in parrots, including within species, suggesting that the node's position may be fluid within a defined area along the alar tract. The coincidence and consistency of these molt sequences in parrots and falcons but in no other order of birds suggests that molt sequence may be a synapomorphic (shared) character state, supporting recent molecular evidence that the Falconiformes and Psittaciformes are sister taxa. A more ancestral molt sequence in *Strigops* may suggest that it split from other parrots prior to a Falconiformes–Psittaciformes divergence or it may indicate reversion to a primitive character state in response to the species' unique nocturnal and ground-dwelling habits. The results of this analysis further suggest that synapomorphic wing-molt sequences can be used as an indicator of systematic relationships in birds and that molt sequence is perhaps controlled by a neurological process more fixed than timing, extent, and geographic location of molts.

Key words: evolution, falcons, molt sequence, parrots, *Strigops*, systematics, synapomorphy.

Implicancias Evolutivas de Secuencias de Muda del Ala Sinapomórficas entre Halcones (Falconiformes) y Loros (Psittaciformes)

Resumen. Examiné más de 4500 especímenes para investigar la significancia evolutiva de la secuencia de la muda en relación con las relaciones sistemáticas de halcones y loros. Los nodos de muda entre las primarias medias (p4–p6) y en s5 entre las secundarias, seguidos por un reemplazo bidireccional desde el nodo interno de cada tracto, fueron confirmados para la mayoría o todas las agrupaciones de halcones y loros, con la excepción de *Strigops habroptila*, que reemplaza sus rémiges en secuencias similares a la mayoría de las otras aves. El inicio de la muda de las primarias varía entre p4 y p5 en los halcones y entre p5 y p6 en los loros, incluso para una misma especie, sugiriendo que la posición del nodo puede ser flexible dentro de un área definida a lo largo del tracto alar. La coincidencia y consistencia de estas secuencias de muda en loros y halcones pero en ningún otro orden de aves sugiere que la secuencia de la muda puede ser un estado de carácter sinapomórfico (compartido), apoyando la evidencia molecular reciente de que los Falconiformes y Psittaciformes son taxa hermanos. Una secuencia de muda más ancestral en *Strigops* puede sugerir que se separó de otros loros antes de una divergencia de Falconiformes–Psittaciformes o puede indicar una reversión a un estado de carácter primitivo en respuesta a los hábitos nocturnos y terrestres únicos de la especie. Los resultados de este análisis sugieren adicionalmente que las secuencias de muda del ala sinapomórficas pueden ser usadas como un indicador de relaciones sistemáticas en las aves y que la secuencia de la muda está tal vez controlada por un proceso neurológico más fijado que el momento, la extensión y la localización geográfica de las mudas.

INTRODUCTION

Molt strategies in birds include four major components: timing, extent, geographic location, and sequence. The first three of these components appear to be quite plastic, varying substantially within genera, species, and even individuals from year to year. For example, such closely related taxa as the

American (*Pluvialis dominica*) and Pacific (*P. fulva*) golden-plovers differ substantially in temporal-spatial strategies and extents of molts, and these differences have been suggested as factors driving speciation of these two taxa (Johnson 1985; see also Rohwer and Irwin 2011). However, even within monotypic species such as the Black-bellied Plover (*P. squatarola*), the timing, extent, and location of molt can vary substantially

Manuscript received 9 November 2012; accepted 16 January 2013.

¹E-mail: ppyle@birdpop.org

according to the latitude or hemisphere of a bird's winter grounds, the result of varying environmental constraints (Serra et al. 1999, Pyle 2008). Several species of passerines also vary intraspecifically and annually in timing and location of pre-basic molt according to location of breeding within eastern or western North America (Rohwer et al. 2005, 2011a) or in response to breeding and climatic factors affecting individuals undertaking molt-migration to the Mexican monsoon region (Pyle et al. 2009). The timing, extent, and location of molts are thought to be driven primarily by hormonal endocrinological processes, as related to timing and status of breeding, available nutritional resources, light regimes, and other environmental factors (Voitkevitch 1966, Payne 1972, Dawson 2006).

The sequence of wing-feather replacement during molt, however, appears to show substantially less phylogenetic variability. For example, the vast majority of birds that replace primaries sequentially do so distally, from the innermost (p1) to the outermost (p9 or p10) primary (Stresemann and Stresemann 1966). When exceptions to this sequence occur, as in the albatrosses (Diomedidae), herons (Ardeidae), owls (Strigidae), and hummingbirds (Trochilidae), an identical or similar variant sequence appears to be maintained among most or all genera and species of the higher taxon (Wagner 1955, Howell 2006, Rohwer and Edwards 2006, Pyle 1997, 2008). Mechanisms controlling the sequence of feather replacement during birds' molt are unknown; both endocrinological and neurological processes have been suggested as determining locations of molt initiation (hereafter "nodes") and sequences within the remiges (Voitkevitch 1966, Bridge 2011, Rohwer et al. 2011b).

Falcons (Falconidae) have long been known to molt their remiges in an atypical sequence, replacing them in two series proceeding bidirectionally (both distally and proximally) within both the primaries (p4 or p5 nodal) and secondaries (s5 nodal) (Fig. 1A); this sequence differs from the more typical distal replacement of primaries (p1 to p10) and proximal molt of outer secondaries (from s1 and s5) shown by accipitrid hawks (Bond 1936, Miller 1941, Pyle 2005) and many other birds (Pyle 1997, 2008). This atypical wing-molt sequence is well documented within the genera *Falco* and *Caracara* (Cramp and Simmons 1980, Marchant and Higgins 1993, Pyle 2008), but sequences within other genera of the Falconidae are poorly known. Likewise, there is scattered evidence that parrots (Psittaciformes) may replace their primaries bidirectionally from a medial node (Dickey and van Rossem 1938, Stresemann and Stresemann 1966, Holyoak 1973, Wyndham 1981, Higgins 1999, Snyder and Russell 2002), but the molt strategies of parrots worldwide, including the sequence of replacement of the secondaries, are poorly documented.

Recent molecular phylogenetic analyses indicate that falcons (Falconiformes, as recently restricted to the Falconidae) and parrots (Psittaciformes) are more closely related than previously supposed (Hackett et al. 2008, Wright et al. 2008, Chesser et al. 2012). To investigate the evolutionary significance of molt sequences as related to these recent taxonomic

suggestions, I examined specimens of falcons and parrots to document consistency of molt sequences in taxonomic divisions of each group and to investigate how these sequences compare to each other and to those of other birds.

METHODS

I examined specimens representing most of the 65 species of falcons and 374 species of parrots (taxonomy following Gill and Donsker 2012) located in seven collections in the United States:

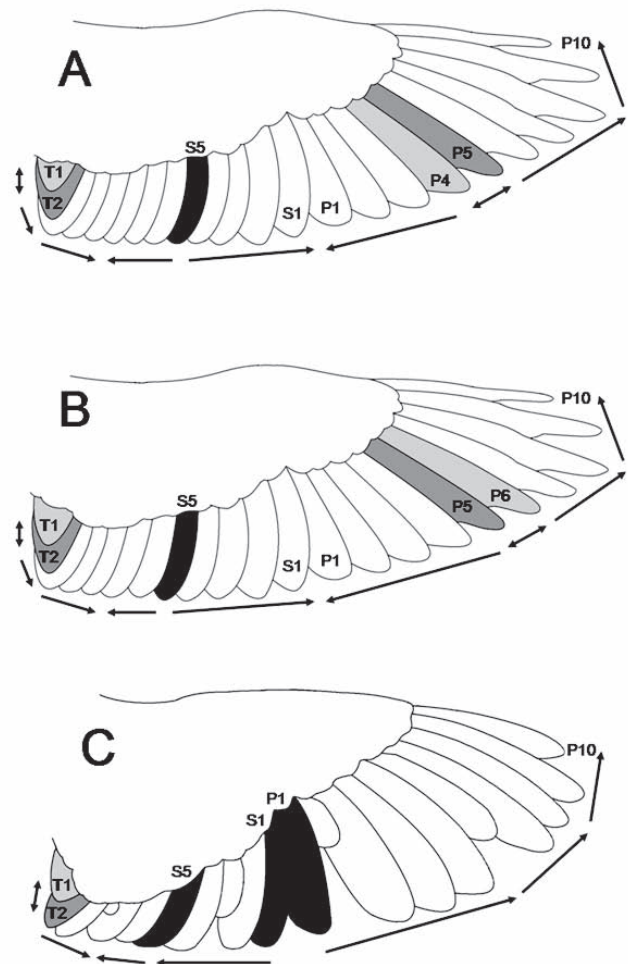


FIGURE 1. Molt sequences of the primaries (P), secondaries (S), and tertials (T) of falcons (A), most parrots (B), and *Strigops habroptila* (C). Shading indicates nodal feathers and arrows represent direction of molt; see text for feather numbering. Falcons have 12 or 13 (shown) secondaries, and most parrots have 12 secondaries (shown), with some smaller species having 10 or 11 (including *Strigops*) secondaries. Apparent patterns of molt in *Strigops* (C) based on specimens AMNH 70781 (primaries; Table II) and CAS 66973 (secondaries, Table 4I).

the Yale Peabody Museum (YPM), New Haven, Connecticut; the National Museum of Natural History (USNM), Washington, D.C.; the Museum of Vertebrate Zoology (MVZ), Berkeley, California; the California Academy of Sciences (CAS), San Francisco, California; the Natural History Museum of Los Angeles County (LACM), Los Angeles, California; the San Diego Natural History Museum (SDNHM), San Diego, California; and the American Museum of Natural History (AMNH), New York. I assessed molt of the primaries on all parrot specimens at YPM, molt of primaries on all falcon and parrot genera at USNM, molt of both primaries and secondaries on all falcon and parrot specimens at MVZ and CAS, and molt of primaries and/or secondaries on selected parrot specimens at LACM, SDNHM, and AMNH to fill gaps in data. My goal was to determine the sequences of replacement of both primaries and secondaries in as many genera of falcons and parrots as possible, subsequently in as many species as possible. I divided the parrots into eight taxonomic groupings based on the clades proposed by Wright et al. (2008). I examined over 4500 specimens for this study, over 1200 falcons and over 3300 parrots.

For each specimen I examined patterns of molt among the primaries (p), secondaries (s), and/or tertials (t), attempting to identify nodes and sequences of replacement within these tracts (see Pyle 2005 for details). Specifically, I assessed whether or not the prebasic molt is initiated medially within each tract and whether or not sequence proceeds bidirectionally from the node. I numbered primaries distally (from innermost p1 to outermost p10), secondaries proximally (from outermost s1 toward the tertials), and the three tertials present in falcons and parrots distally (from innermost t1 to outermost t3). The number of secondaries varies from 10 to 12 in parrots and 12 to 13 in falcons, with the added or subtracted secondaries (evolutionarily) apparently occurring between s7 and the tertials (see Edwards and Rohwer 2005); thus this system of numbering appears to preserve homology of both inner secondaries (s1–s7) and tertials (t1–t3).

I determined nodes and replacement sequences by the methods of Rohwer (2008), including development of raw-data examples and iterated-data summaries; data from right wings are shown although I examined left wings also to confirm that molt was symmetrical. Breeding adults of both falcons and parrots can suspend molt, and the prebasic molt of certain large parrots can be incomplete (Stresemann and Stresemann 1966, Higgins 1999). In species showing suspended and/or incomplete replacement I analyzed molt patterns carefully to identify the original node and sequence, prior to suspension (see Pyle 2005 for details). To confirm node and sequence I present only data from individuals in active molt, although I also used the difference in wear between adjacent full-grown feathers to determine the direction of replacement (Rohwer 2008). For example, if p5 appeared more worn than both p4 and p6, I considered p5 nodal and the sequence bidirectional. I restricted analyses to data from birds collected in active molt, which increased accuracy by ensuring that assessment was based only on more

recently replaced feathers, in which relative wear was more easily determined. Because few birds in active molt have been collected, <8% of specimens that I examined could be used to confirm nodes and/or sequence.

RESULTS

I documented medial nodes, at p4, p5, or p6, in 46 specimens of falcons and 190 of parrots, and I documented sequential bidirectional replacement from one of these medial nodes in 50 specimens of falcons and 231 of parrots (Tables 1, 2, Fig. 1A, B). With the exception of one genus of parrot (*Strigops*), I found no evidence of proximal replacement from p10 to p6 or distal replacement from p1 to p4 in any falcon or parrot (Table 2). I confirmed a medial node and/or bidirectional replacement from a medial node in all 11 genera and 35 of 65 species of falcons, and in eight of nine taxonomic groupings (all except *Strigops*), 85 of 89 genera, and 180 of 374 species of parrots (Table 3).

Among the falcons, 34 specimens (23 species of 9 genera) had initiated molt at p5 (e.g., Table 1A, C), 12 specimens (7 species of 3 genera) had initiated molt at p4 (e.g., Table 1B), and in 12 specimens I could not identify the node (e.g., Tables 1D 2A). For these last 12 specimens, either the degree of wear of p4 and p5 was similar (5 specimens; e.g., Table 1D) or both p4 and p5 were growing and of approximately the same length (7 specimens of 5 species of *Microhierax* and *Falco*). Examples of the latter included CAS 23836 (*M. fringillaris*) and MVZ 32260 (*F. mexicanus*), with both p4 and p5 dropped synchronously on both wings, and CAS 67679 (*F. amurensis*), with both p4 and p5 growing and of equal length (Table 1E). I confirmed a node at either p4 or p5 in five species of three genera, *Ibycter*, *Caracara*, and *Falco* (e.g., Table 1A, B); for example, specimens of *F. sparverius* had p5 nodal (MVZ 19796 and 19797), p4 nodal (MVZ 32276), or both p4 and p5 growing synchronously or nearly so (MVZ 19795, 26714, and 79522). I observed no evidence for nodes apart from p4 or p5 in the 11 genera and 65 species of falcons (Tables 2, 3) and, in contrast to the parrots (see below), I did not observe multiple waves in any falcon (cf. Pyle 2005).

Among the parrots, 107 specimens (80 species of 7 taxonomic groupings, all but *Strigops*) had initiated molt at p5 (e.g., Table 1F), 83 specimens (58 species of 6 groupings, all but *Strigops* and *Psittichas*) had initiated molt at p6 (e.g., Table 1G), and in 74 specimens I could not identify a node (e.g., Table 1H) (Table 2B). In contrast to the falcons, I examined no parrots that appeared to have initiated molt from both nodal feathers (p5 and p6) synchronously; however, as in the falcons, I found the point of initiation to vary between p5 or p6 within at least 9 species (4 groupings). Examples are *Nestor notabilis* (p5 nodal in CAS 32944, AMNH 202984, and LACM 58466; p6 nodal in AMNH 202986), *Trichoglossus hamatodus* (p5 nodal in YPM 99612 and MVZ 89568; p6 nodal in CAS 24362 and CAS 24363), and *Ara militaris* (p5

TABLE 1. Examples of different primary-molt sequences of falcons and parrots, based on data from specimens selected to represent different taxa and collections. Table designed after Rohwer (2008): primaries (P) are indicated as new, old, intermediate, or growing, in the last case to the nearest one-tenth of feather length (missing indicated by "0.1"), arrows indicate direction of replacement, and "N" indicates the nodal feather from which replacement commenced. "Susp" indicates feathers replaced before a suspension of molt; "int" indicates a separate generation of feathers intermediate between old and new, in species with incomplete molts.

Specimen ^a	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
Falcons										
A				←	N	→	→			
	old	old	old	new	new	0.8	0.1	old	old	old
B			←	N	→	→	→			
	old	old	0.5	new	new	0.6	0.1	old	old	old
C	←	←	←	←	N	→	→	→	→	→
	0.1	0.7	new	new	susp	new	new	new	0.9	0.6
D			←	N?	N?	→				
	old	old	0.3	new	new	0.4	old	old	old	old
E				N	N	→				
	old	old	old	0.5	0.5	0.1	old	old	old	old
Parrots										
F		←	←	←	N	→	→	→		
	old	susp	int	int	0.1	int	int	susp	old	old
G					←	N	→			
	old	old	old	old	0.1	new	0.2	old	old	old
H	←	←	←	←	N?	N?	→	→	→	→
	0.3	0.9	new	new	susp	susp	new	new	0.8	0.1
I	N?	→		→?	→	→		→?	→	→
	new	0.4	old	int	new	0.7	old	int	new	new
J	N?		→	→		→	→	→	→	
	new	old	int	new	old	int	int	new	new	old

^aSpecimens on which data were based: A, *Falco rufogularis* (MVZ 155578); B, *Falco rufogularis* (MVZ 70393); C, *Ibycter americanus* (CAS 34169); D, *Spizaipteryx circumcinctus* (USNM 283728); E, *Falco amurensis* (CAS 67679); F, *Psittichas fulgidus* (LACM 17533; see also Table 4F); G, *Ara manilata* (SDNHM 31985); H, *Cyanoramphus auriceps* (CAS 85044); I, *Strigops habroptila* (AMNH 707871); J, *Strigops habroptila* (CAS 83750).

TABLE 2. Count summary and iteration of raw molt scores for primaries of falcons and parrots. Data presentation follows Rohwer (2008) and includes all specimens in which sequence and/or node were confirmed. Counts for observed nodes at each primary and documented occurrences of sequence between primaries based on specimens collected while in active molt; see Table 1 for examples. Note that samples include some specimens for which either node or directionality, but not both, could be confirmed (see text).

Strategy	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
Falcons										
Nodal	0	0	0	12	34	0	0	0	0	0
Direction →	0	0	0	10	33	24	20	15	11	
Direction ←	10	24	34	30	0	0	0	0	0	
Direction ?	0	0	0	12	0	0	0	0	0	
Terminal	10	0	0	0	0	0	0	0	0	11
Parrots ^a										
Nodal	0	0	0	0	107	83	0	0	0	0
Direction →	0	0	0	0	102	20	16	10	80	
Direction ←	64	10	15	19	67	1	1	3	0	
Direction ?	0	8	6	4	74	0	0	0	0	
Terminal	64	0	0	0	0	0	0	0	0	80

^aAll parrots with the exception of genus *Strigops*.

TABLE 3. Genera and species of falcons and parrots with confirmed molt nodes among the primaries and secondaries, from which bidirectional replacement sequences commence.

Taxon ^a	Genera confirmed ^b		Species confirmed ^b		Voucher ^c
	Primaries	Secondaries	Primaries	Secondaries	
Falcons					
<i>Daptrius</i>	1/1	1/1	1/1	1/1	USNM 206394
<i>Ibycter</i>	1/1	1/1	1/1	1/1	MVZ 140626
<i>Phalcoboenus</i>	1/1	1/1	2/4	1/4	USNM 614838
<i>Caracara</i>	1/1	1/1	2/2	1/2	MVZ 144754
<i>Milvago</i>	1/1	1/1	1/2	1/2	USNM 372375
<i>Herpetotheres</i>	1/1	1/1	1/1	1/1	MVZ 83997
<i>Micrastur</i>	1/1	1/1	3/7	1/7	MVZ 97789
<i>Spizapteryx</i>	1/1	0/1	1/1	0/1	USNM 283728
<i>Poliheirex</i>	1/1	1/1	2/2	1/2	CAS 34475
<i>Microhierex</i>	1/1	1/1	4/5	2/5	USNM 179080
<i>Falco</i>	1/1	1/1	18/39	10/39	CAS 60927
Total	11/11	10/11	35/65	20/65	
Parrots					
<i>Nestor</i>	1/1	1/1	2/2	1/2	SDNHM 47859
<i>Strigops</i>	0/1	0/1	0/1	0/1	
Cacatuidae	7/7	3/7	11/21	3/21	YPM 41692
<i>Psittrichas</i>	1/1	1/1	1/1	1/1	AMNH 620926
Old World clade	41/42	15/42	84/174	22/174	USNM 277318
<i>Coracopsis</i>	1/1	0/1	2/2	0/2	USNM 484079
<i>Psittacus/Poicephalus</i>	2/2	1/2	6/11	2/11	MVZ 70204
New World clade	32/34	20/34	74/162	23/162	CAS 65829
Total	85/89	41/89	180/374	52/374	

^aTaxa include all 11 genera and 65 species of falcons (following Gill and Donsker 2012) and eight taxonomic groupings (based on clades of Wright et al. 2008; see text) comprising 89 genera and 374 species of parrots (following Gill and Donsker 2012).

^bNumber confirmed/total number genera and species of each taxon reported. "Confirmed" indicates at least one specimen of the taxon was examined with molt node at p4, p5, or p6 (primaries) or s5 (secondaries) and/or with bidirectional replacement from this node.

^cSee also text and Tables 1 and 4 for additional specimen examples.

nodal in MVZ 109606; p6 nodal in MVZ 116419). Also, as in the falcons (Pyle 2005), I observed suspension of molt (e.g., after p5 and p6 had been replaced, perhaps during breeding; e.g., Table 1H) in at least 37 species. In some species such as *Nestor* (e.g., AMNH 202984 and SDNHM 47859), *Nymphicus* (e.g., YPM 41675), *Psittrichas* (e.g., CAS 32945 and LACM 17553, Table 1F), *Psittacus* (e.g., MVZ 45015), and *Ara* (e.g., CAS 85514), molts could be incomplete and/or proceed in multiple waves from the node, as has been previously reported in large parrots (Stresemann and Stresemann 1966, Higgins 1999). Careful assessment of patterns of feather wear and molt in these specimens revealed a similar underlying molt sequence from nodes at p5 or p6 but that the replacement of remiges had simply been arrested and resumed in sequence during the subsequent molt, as in Staffeldmauser (Pyle 2005, 2006, 2008). I could not confirm the nodal primary and sequence of molt in one taxonomic group (*Strigops*; see below); otherwise, I observed no evidence of

molt nodes apart from p5 or p6 or of any other molt strategy among the remaining 373 species, 88 genera, and seven taxonomic groupings of parrots (Tables 1–3).

With respect to the secondaries, I found 81 specimens (22 of falcons and 59 of parrots) with molt commencing at s5 and proceeding bidirectionally (Fig. 1A, B). In an additional 19 specimens (4 of falcons and 15 of parrots) I confirmed a node at s5 but not bidirectional replacement (Tables 4, 5). With the possible exception of *Strigops* (see below), I documented no other nodes or sequences among the distal secondaries (s1–s7) of either group (Table 5). Among both falcons and parrots, however, there was evidence for a second node among the tertials (Table 5), most commonly (approximately 85% of falcons and 76% of parrots) at the medial tertial (t2) (e.g., Table 4A, C, E–H) but sometimes (15% of falcons and 24% of parrots) at the innermost tertial (t1) (e.g., Table 4B). The position of this node was often undeterminable or suggested synchronous replacement (e.g., Table 4D). Proximal replacement from the tertials met

distal replacement from s5, resulting in a terminus between s7 and s10, the terminal position depending, in part, on the number of secondaries in the species (Tables 4, 5).

In their secondaries, some larger parrots showed evidence of incomplete molt and multiple waves of molt (e.g., Table 4G), as in their primaries, but there was no evidence for proximal replacement of the outer secondaries (s1 to s4, with the exception of *Strigops*) or distal replacement from s8 to s5 (Table 5B). I confirmed bidirectional replacement from s5 in 10 of 11 genera of falcons, all but *Spizapteryx* (of which I examined no specimens collected in active secondary molt) and in six of eight taxonomic groupings of parrots, all but *Strigops* and *Coracopsis* (the latter of which I examined no specimens in active secondary molt). I also confirmed bidirectional replacement from s5 in 20 of 65 species of falcons and 41 of 89 genera and 52 of 374 species of parrots (Table 3).

The sequences of molt of the primaries and secondaries in the flightless and nocturnal *Strigops habroptila* (Kakapo or Owl Parrot) apparently differ from those of other parrots (Fig. 1C, Tables 1I, J, 4I, J). Of the 50 specimens I examined, seven were collected during active primary molt, five were in active

secondary molt, and both molting and nonmolting specimens generally showed multiple waves of distal replacement in patterns like Staffellauser (Pyle 2005, 2006). Molt appeared to proceed slowly (no specimens had adjacent remiges growing at the same time), and the feathers of *Strigops* being softer than those of other parrots hindered identification of replacement patterns by wear; a slow rate of molt may have obscured detection of medial nodes. Most or all evidence, however, suggested that the primaries were replaced from p1 to p10 and that the secondaries were replaced proximally from s1 and s5 and distally from the tertials (Fig. 1C). For example, AMNH 707871 showed p2 and p6 growing, with apparent distal clines from p3 to p5 and from p7 to p10 (Fig. 1C, Table 1I), and CAS 83750 showed Staffellauser-like sets and clines including newer p1, older p2 to newer p4, older p5 to newer p9, and older p10 (Table 1J). Specimens of *Strigops* indicating proximal rather than distal replacement from s1 to s5 included CAS 66973 (s2 newer than s1, s3 growing, and s4 older than s5; Fig. 1C, Table 4I) and CAS 83750, MVZ 44293 (Table 4J), and LACM 16064, which were not in active molt but showed apparent clines from older s1 to newer s4 and older s5 proximally to at least s7. The sequence of

TABLE 4. Examples of different secondary-molt sequences of falcons and parrots based on data from specimens selected to represent different collections and taxa. Table designed after Rohwer (2008) for secondaries (S, numbered proximally from innermost) and tertials (T, numbered distally from innermost); see Table 1 for abbreviations. The column for “S8–X” represents secondaries between S7 and the tertials, which vary in number from 0 (some parrot taxa with 10 secondaries), to 3 (most falcons with 13 secondaries); “n/o” or “i/o” indicates these feathers were new, intermediate, old, and/or growing in condition.

Specimen ^a	S1	S2	S3	S4	S5	S6	S7	S8–X	T3	T2	T1
Falcons											
A				←	N	→	→		←	N	→
	old	old	old	.8	new	new	.8	old	.1	new	new
B		←	←	←	N	→	→	→T←	←	←	N
	old	.1	new	new	susp	new	new	n/o	new	new	new
C				←	N	→	→			N	→
	old	old	old	.1	new	.5	.1	old	old	.5	.1
Parrots											
D				←	N	→	→		←	N?	N?
	old	old	old	susp	new	new	susp	old	susp	new	new
E		←	←	←	N	→	→	→T←	←	N	→
	old	.9	new	new	new	new	new	n/o	new	new	new
F				←	N	→	→		←	N	→
	old	old	old	.9	new	.4	old	old	.9	new	new
G		←	←	←	N	→	→	→T←	←	N	→
	old	int	int	int	susp	int	int	i/o	int	susp	int
H				←	N	→	→	→T←	←	N	→
	old	old	.9	new	new	new	.8	n/o	new	new	new
I	N?	→	→		N?	→	→	→T←	←	N?	N?
	new	new	.8	old	new	new	new	n/o	new	new	new
J		→	→	→	N?	→	→	→T←	←	←	N
	old	int	int	int	new	.1	.1	i/o	new	new	new

^aSpecimens on which data were based: A, *Falco tinnunculus* (MVZ 21355); B, *Ibycter americanus* (CAS 34169); C, *Herpetotheres cachinans* (MVZ 83997); D, *Nestor notabilis* (CAS 34532); E, *Cacatua galerita* (CAS 24372); F, *Psittichas fulgidus* (LACM 17533; see also Table 1F); G, *Poiccephalus meyeri* (MVZ 136778); H, *Amazona albifrons* (MVZ 142428); I, *Strigops habroptila* (CAS 66973); J, *Strigops habroptila* (MVZ 44293).

TABLE 5. Count summary and iteration of raw molt scores (Rohwer 2008) for secondaries (S, numbered proximally from outermost) and tertials (T, numbered distally from innermost) of falcons and parrots. Data include all specimens in which sequence and/or node were confirmed. Counts for observed nodes at each primary and documented occurrences of sequence between primaries based on specimens collected while in active molt. See Table 4 for examples and regarding feather numbering and column "S8-X." Note that samples include some specimens for which either node or directionality, but not both, could be confirmed (see text).

Strategy	S1	S2	S3	S4	S5	S6	S7	S8-X	T3	T2	T1
Falcons											
Nodal	0	0	0	0	26	0	0	0	0	17	3
Direction →	0	0	0	0	23	18	15	0	0		
Direction ←	5	10	17	22	0	0	0	17	22	13	
Direction ?	0	0	0	0	0	0	0	0	0	2	
Terminal	4	0	0	0	0	0	0	15	0	6	13
Parrots ^a											
Nodal	0	0	0	0	74	0	0	0	0	45	13
Direction →	0	0	0	0	57	40	23	0	0		
Direction ←	1	22	37	56	0	0	0	31	46	40	
Direction ?	0	0	0	0	0	0	0	0	0	11	
Terminal	10	0	0	0	0	0	0	23	0	16	40

^aAll parrots with the exception of genus *Strigops*.

replacement of the inner secondaries (tertials to s7) in *Strigops* appeared to be similar to that of other parrots and falcons, with indication of a node at the inner two tertials and waves meeting at s7 or s8 of 11 secondaries (Fig. 1C, Table 4I, J).

DISCUSSION

With the exception of *Strigops*, falcons and parrot consistently show nodes in the medial portions of the primaries and secondaries, and bidirectional replacement from both of these nodes (Fig. 1A, B). Both groups initiate molt at p5 in a majority of cases. Previous suggestions of nodes at p3, p4, p7, or p8 in parrots (e.g., Holyoak 1973, Wyndham 1981, Higgins 1999) and falcons (e.g., Dement'ev and Gladkov 1951) were probably based on individuals that had suspended molt after replacing at least p5 and p6 (parrots) or p4 and p5 (falcons) for breeding or on parrots with multiple waves of replacement. Among this latter group, incomplete molt may result in the starting point varying from year to year, but the underlying sequence of replacement appears to be maintained (Rohwer 1999, Pyle 2005, 2006). In the secondaries, both falcons and parrots consistently show a node at s5. Distal replacement from this feather to s1 in all falcons and parrots (excepting *Strigops*) represents a sequence different from that of most or all other birds, whereas the sequence of the inner secondaries including the tertials is similar to many other taxa (Stresemann and Stresemann 1966, Pyle 1997, 2008). The suggestion of H. Hampe (in Stresemann and Stresemann 1966) that parrots molt all their secondaries proximally may have resulted from overlooking distal replacement from s5 to s1 and from the tertials.

That the first feather dropped can be either p4 or p5 in falcons and either p5 or p6 in parrots suggests that the node may not be fixed at a single feather. Replacement of the inner

two tertials (t1–t2) also appears to follow this pattern, with t2 nodal in a majority of cases. This may indicate that the node can fall between two feathers, with either dropping first or both dropping simultaneously, and that the mechanism controlling molt initiation can be plastic with respect to exact position along these alar tracts. In some other species the node varies among more than two primaries, e.g., from p2 to p5 in Savi's Warbler (*Locustella luscinioides*; Neto and Gosler 2006) and from p2 to p4 in the Rufous Fantail (*Rhipidura rufifrons*; Junda et al. 2012), suggesting the location is fluid within a defined area. The position of the node may be plastic and have shifted within the falcons and parrots, perhaps as an adaptive response to differences in wing shape and the time it takes to replace inner (proximal to the node) and outer (distal to the node) primaries, with the ultimate goal of completing primary molt at each terminus (p1 and p10) at approximately the same time. Despite some variation in the placement of the node, that molt proceeds bidirectionally from a medial position within the primaries is atypical of birds.

A survey of the literature and my unpublished data reveals no species of bird other than falcons and parrots replacing both primaries and secondaries bidirectionally from a medial node (Table 6). This survey included at least one species of all 28 other orders of volant birds (according to Gill and Donsker 2012) that do not replace primaries synchronously. Three other orders show bidirectional replacement of primaries and one other order shows bidirectional replacement of secondaries, but none besides parrots and falcons shows this pattern in both tracts (Table 6), a coincidence greater than expected from chance alone (one-tailed Fisher's exact test, $P = 0.032$). The similar wing-molt strategies of falcons and parrots may represent convergence related to the similar

TABLE 6. Orders of birds documented as showing molt nodes in either medial primaries or medial secondaries, along with bidirectional replacement from the node.

Order, group	Primaries	Secondaries	Source
Galliformes	Distal from p1	Node at s3	Warren and Gordon 1935, Pyle 2008
Procellariiformes: albatrosses	Node at p7/p8	Proximal from s1 and s5	Edwards and Rohwer 2005, Howell 2006, Rohwer and Edwards 2006
Falconiformes, falcons	Node at p4/p5	Node at s5	This study
Strigiformes	Node ranging from p3 to p7	Proximal from s1 and s5	Pyle 1997, unpubl. data
Psittaciformes	Node at p5/p6	Node at s5	This study
Passeriformes: shrikes, fantails, dippers, Old-World warblers	Node ranging from p2 to p5	Proximal from s1	Stresemann and Stresemann 1966, Jenni and Winkler 1994, Pyle 1997, Junda et al. 2012

pointed wing shapes and rapid flight of both groups. However, along with the consistency of this molt pattern in these two orders, it suggests that the sequence of remigial molt may be a synapomorphic (shared) character state retained from a common ancestor, a result that would have important evolutionary implications for both avian systematics and avian molt.

Systematically, synapomorphic sequences of remigial molt would support molecular evidence that the Falconiformes and Psittaciformes are sister taxa that diverged during the Cretaceous in the Southern Hemisphere before separation of Gondwanaland (Cracraft 1973, Tavares et al. 2006, Hackett et al. 2008, Wright et al. 2008). Similar molecular evidence suggests that the Passeriformes may also be related to these two orders (Hackett et al. 2008, Wang et al. 2011, Chesser et al. 2012). Although a few species of Old World shrikes, warblers, and flycatchers replace their primaries bidirectionally from a medial node (Jenni and Winkler 1994, Junda et al. 2012), these species do not follow a similar strategy among secondaries, and they are not basal taxa within the Passeriformes (Wang et al. 2011). Most Passeriformes, including basal taxa, replace their primaries distally from p1 to p10, as do most other birds (Sibley and Ahlquist 1990). This suggests that bidirectional molt of the primaries in these passerine exceptions evolved independently and that the Passeriformes may have diverged prior to development of bidirectional remigial molt in the ancestor of the Falconiformes and Psittaciformes.

My observations support those of Higgins (1999) and Powlesland et al. (2006) that the molt sequence of *Strigops* may differ from that of other parrots and falcons. It perhaps follows a Staffelmauser-like pattern that is common to other large species of volant birds apart from falcons and parrots (Fig 1C; Stresemann and Stresemann 1966, Rohwer 1999, Pyle 2006, 2008). *Strigops* and *Nestor* are widely regarded as basal to all other parrots (Wright et al. 2008). A more primitive pattern of molt sequence in *Strigops* suggests that it may have diverged from *Nestor* before falcons diverged from the lineage including *Nestor*. However, it is perhaps more likely that the unusual flightless and nocturnal habits of *Strigops* resulted

in its molt patterns subsequently diverging from those of *Nestor* and other parrots, as have other characters of *Strigops* (Corfield et al. 2011). Bidirectional replacement presumably evolved to allow more rapid and complete molt while maintaining fuller integrity of the wing surface for flight (Pyle 2005). Therefore the selective pressure for this strategy in the flightless *Strigops* may have been lost, resulting in reversion to an ancestral and primitive molt sequence.

Regarding molt strategies, a paired synapomorphy of primaries and secondaries in the Falconiformes and Psittaciformes suggests that the sequence of remigial molt is relatively fixed and may be useful in understanding avian taxonomic relationships (Sibley and Ahlquist 1990). In other orders and families with an atypical sequence of primary molt this trait is consistent in most or all species (Wagner 1955, Howell 2006, Rohwer and Edwards 2006, Pyle 1997, 2008). In the secondaries the patterns also appear to be rather fixed in volant birds, replacement proceeding distally from s1, distally from s5 as well in diastatic species, which have lost a secondary between s4 and s5 evolutionarily, and proximally from the tertials (Sibley and Ahlquist 1990, Pyle 1997, 2008), including an apparent node at the second tertial present in a majority of passerines (G. David, P. Pyle, unpubl. data). Only the diastatic parrots and falcons (replacement proceeding from a node at s5) and the eutaxic Galliformes (replacement proceeding from a node at s3) represent exceptions reported thus far, and in all three of these groups the pattern appears to be maintained by all subtaxa within these orders (with the exception of *Strigops*).

My study suggests a role for sequences of remigial molt in systematics, and I recommend further investigation of this, along with the role of other forms of wing taxis, such as diastaticity (Sibley and Ahlquist 1990, Bostwick and Brady 2002) and the number of primaries or rectrices. For example, the grebes (Podicipediformes) and flamingos (Phoenicopteriformes) are unusual in having 11 functional primaries, and these two groups have recently been reported to be closely related (Hackett et al. 2008); the number of rectrices may have taxonomic implications for wrens and other birds (Winker

2012); and presence/absence of a tenth primary may have taxonomic implications within the Passeriformes (Sibley and Ahlquist 1990). The number of secondaries, by contrast, shows more variation within families (Pyle 2008) and even within species of larger birds (Edwards and Rohwer 2005).

A consistent sequence of remigial molt within higher taxa of birds such as falcons and parrots also suggests that the mechanisms controlling molt nodes and sequence of replacement within tracts may be more fixed than those controlling the timing, extent, and geographic location of molts. Voitkevitch (1966:250–263) summarized evidence that molt sequence may be influenced, at least in part, by a relatively fixed neurological as opposed to a more plastic endocrinological process (cf. Lesells 2008), the latter appearing to play a greater role in controlling the timing, extent, and location of molt (Voitkevitch 1966, Payne 1972, Dawson 2006, Bridge 2011). Further investigation into mechanisms of molt sequence is needed (Bridge 2011, Rohwer et al. 2011b), but the results of this analysis suggest that the sequence shows more synapomorphy and is thus a better indicator of systematic relationships in birds than is the timing, location, and extent of molt (Johnson 1985, Rohwer and Irwin 2011). A better understanding of the genetic basis for initiation and sequence of molt will be needed for this possibility to be addressed.

ACKNOWLEDGMENTS

I thank the curators and managers of the bird specimen collections at the American Museum of Natural History (Mary LeCroy and Paul Sweet), California Academy of Sciences (Jack Dumbarton and Maureen Flannery), Museum of Vertebrate Zoology (Carla Cicero), Natural History Museum of Los Angeles County (Kimball Garrett), San Diego Natural History Museum (Philip Unitt), United States Museum of Natural History (Storrs Olson and James Dean), and Yale Peabody Museum (Kristof Zyskowski) for assistance examining specimens; Rowena Forest assisted me in recording data. A travel grant from the University of California, Davis (UCD11-02122) facilitated my visit to eastern North American museums for this and other specimen-based research. I also thank John Bates and Josh Engel of the Field Museum of Natural History, Chicago, for spurring me to perform this analysis. I am grateful to Siobhan Ruck for preparing the illustrations in Figure 1, and to Eli Bridge, Sievert Rohwer, Luke Butler and an anonymous reviewer for helpful suggestions on the manuscript. This is contribution 455 of The Institute for Bird Populations.

LITERATURE CITED

BOND, R. M. 1936. Molting of hawks, with special regard to the Duck Hawk. *Condor* 38:119–120.

BOSTWICK, K. S., AND M. J. BRADY. 2002. Phylogenetic analysis of wing feather taxis in birds: macroevolutionary patterns of genetic drift? *Auk* 119:943–954.

BRIDGE, E. 2011. Mind the gaps: what's missing in our understanding of feather molt. *Condor* 113:1–4.

CHESSER, R. T., R. C. BANKS, F. K. BARKER, C. CICERO, J. L. DUNN, A. W. KRATTER, I. J. LOVETTE, P. C. RASMUSSEN, J. V. REMSEN JR., J. D. RISING, D. F. STOTZ, AND K. WINKER. 2012. Fifty-third supplement to the American Ornithologists' Union *Check-List of North American Birds*. *Auk* 129:573–588.

CORFIELD, J. R., A. C. GSELL, D. BRUNTON, C. P. HEESY, M. I. HALL, M. L. ACOSTA, AND A. N. IWANIUK [ONLINE]. 2011. Anatomical specializations for nocturnality in a critically endangered parrot, the Kakapo (*Strigops habroptilus*). *PLoS One* 6(8):e22945. <<http://www.plosone.org/article/info:doi/10.1371/journal.pone.0022945>>.

CRACRAFT, J. 1973. Continental drift, paleoclimatology, and the evolution and biogeography of birds. *Journal of Zoology* 169:455–545.

CRAMP, S., AND K. E. L. SIMMONS [EDS.]. 1980. The birds of the western Palearctic, vol. II. Oxford University Press, Oxford, England.

DAWSON, A. 2006. Control of molt in birds: association with prolactin and gonadal regression in starlings. *General and Comparative Endocrinology* 147:314–322.

DEMENT'EV, G. P., AND N. A. GLADKOV [EDS.]. 1951. Birds of the Soviet Union, vol. I. Gosudarstvennoe Izdatel'stvo Sovetskaya Nauka, Moscow [English translation, Israel Program for Scientific Translations, 1968].

DICKEY, D. R., AND A. J. VAN ROSSEM. 1938. The birds of El Salvador. Zoological Series of the Field Museum of Natural History 23:1–609.

EDWARDS, A. E., AND S. ROHWER. 2005. Large-scale patterns of molt activation in the flight feathers of two albatross species. *Condor* 107:835–848.

GILL, F., AND D. DONSKER [EDS., ONLINE]. 2012. IOC world bird names, version 2.11. <<http://www.worldbirdnames.org/>> (10 January 2012).

HACKETT, S. J., R. T. KIMBALL, S. REDDY, R. C. BOWIE, E. L. BRAUN, M. J. BRAUN, J. L. CHOJNOWSKI, W. A. COX, K. HAN, J. HARSHMAN, C. D. HUDDLESTON, B. D. MARKS, K. J. MIGLIA, W. S. MOORE, F. H. SHELDON, D. W. STEADMAN, C. C. WITT, AND T. YURI. 2008. A phylogenomic study of birds reveals their evolutionary history. *Science* 320:1763–1768.

HIGGINS, P. J. [ED.]. 1999. Handbook of Australian, New Zealand and Antarctic birds, vol. 4. Oxford University Press, Melbourne.

HOLYOAK, D. T. 1973. Comments on taxonomy and relationships in the parrot subfamilies Nestorinae, Loriinae, and Platycercinae. *Emu* 73:157–176.

HOWELL, S. N. G. 2006. Primary molt in the Black-footed Albatross. *Western Birds* 37:241–244.

JENNI, L., AND R. WINKLER. 1994. Molt and ageing of European passerines. Academic Press, New York.

JOHNSON, O. W. 1985. Timing of primary molt in first-year golden-plovers and some evolutionary implications. *Wilson Bulletin* 97:237–239.

JUNDA, J., A. L. CRARY, AND P. PYLE. 2012. An age-specific, bivariate pattern to replacement of primaries during the prebasic molt in Rufous Fantail (*Rhipidura rufifrons*). *Wilson Journal of Ornithology* 124:680–685.

LESSELLS, K. 2008. Neuroendocrine control of life histories: what do we need to know to understand the evolution of phenotypic plasticity? *Philosophical Transactions of the Royal Society B* 363:1589–1598.

MARCHANT, S., AND P. J. HIGGINS [EDS.]. 1993. Handbook of Australian, New Zealand, and Antarctic Birds, vol. 2. Oxford University Press, Melbourne.

MILLER, A. H. 1941. The significance of molt centers among secondary remiges in the Falconiformes. *Condor* 43:113–115.

NETO, J. M., AND A. G. GOSLER. 2006. Post-juvenile and post-breeding moult of Savi's Warblers *Locustella luscinioides* in Portugal. *Ibis* 148:39–49.

PAYNE, R. B. 1972. Mechanisms and control of molt, p. 103–105. In D. S. Farner and J. R. King [EDS.], *Avian biology*, vol. 2. Academic Press, New York.

- POWLESLAND, R. G., D. V. MERTON, AND J. F. COCKREM. 2006. A parrot apart: the natural history of the Kakapo (*Strigops habroptilus*), and the context of its conservation management. *Notornis* 53:3–26.
- PYLE, P. 1997. Identification guide to North American birds, part 1. Slate Creek Press, Bolinas, CA.
- PYLE, P. 2005. Remigial molt patterns in North American Falconiformes as related to age, sex, breeding status, and life-history strategies. *Condor* 107:823–834.
- PYLE, P. 2006. Staffeldmauser and other adaptive wing-molt strategies in larger birds. *Western Birds* 37:179–185.
- PYLE, P. 2008. Identification guide to North American birds, part 2. Slate Creek Press, Point Reyes Station, CA.
- PYLE, P., W. A. LEITNER, L. LOZANO-ANGULO, F. AVILEZ-TERAN, H. SWANSON, E. GÓMEZ-LIMÓN, AND M. K. CHAMBERS. 2009. Temporal, spatial, and annual variation in the occurrence of molt-migrant passerines in the Mexican monsoon region. *Condor* 111:583–590.
- ROHWER, S. 1999. Time constraints and moult–breeding tradeoffs in large birds. *Proceedings of the International Ornithological Congress* 22:568–581.
- ROHWER, S. 2008. A primer on summarizing molt data for flight feathers. *Condor* 110:799–806.
- ROHWER, S., AND A. E. EDWARDS. 2006. Reply to Howell on primary molt in albatrosses. *Western Birds* 37:245–247.
- ROHWER, S., AND D. E. IRWIN. 2011. Molt, orientation, and avian speciation. *Auk* 128:419–425.
- ROHWER, S., L. K. BUTLER, AND D. FROEHLICH. 2005. Ecology and demography of east–west differences in molt scheduling of neotropical migrant passerines, p. 87–105. *In* R. Greenberg and P. P. Marra [EDS.], *Birds of two worlds: the ecology and evolution of migratory birds*. Johns Hopkins University Press, Baltimore.
- ROHWER, S., K. A. HOBSON, AND S. YANG. 2011a. Stable isotopes (δD) reveal east–west differences in scheduling of molt and migration in Northern Rough-winged Swallows. *Auk* 128:622–530.
- ROHWER, S., A. VIGGIANO, AND J. M. MARZLUFF. 2011b. Reciprocal tradeoffs between molt and breeding in albatrosses. *Condor* 113:61–70.
- SERRA, L., D. A. WHITELAW, A. J. TREE, AND L. G. UNDERHILL. 1999. Molt, mass and migration of Grey Plovers *Pluvialis squatarola* wintering in South Africa. *Ardea* 87:71–81.
- SIBLEY, C. G., AND J. E. AHLQUIST. 1990. Phylogeny and classification of birds: a study in molecular evolution. Yale University Press, New Haven, CT.
- SNYDER, N. F., AND K. RUSSELL. 2002. Carolina Parakeet (*Conuropsis carolinensis*), no. 667. *In* A. Poole and F. Gill [EDS.], *The birds of North America*. Birds of North America, Inc., Philadelphia.
- STRESEMANN, E., AND V. STRESEMANN. 1966. Die Mauser der Vögel. *Journal für Ornithologie* 107:1–448.
- TAVARES, E. S., A. J. BAKER, S. L. PEREIRA, AND C. Y. MIYAKI. 2006. Phylogenetic relationships and historical biogeography of neotropical parrots (Psittaciformes: Psittacidae: Arini) inferred from mitochondrial and nuclear DNA sequences. *Systematic Biology* 55:454–470.
- VOITKEVICH, A. A. 1966. The feathers and plumage of birds. English translation, October House, New York.
- WAGNER, H. O. 1955. The molt of hummingbirds. *Auk* 72:286–291.
- WANG, N., E. L. BRAUN, AND R. T. KIMBALL. 2011. Testing hypotheses about the sister group of the Passeriformes using an independent 30 locus dataset. *Molecular Biology and Evolution* 29:737–750.
- WARREN, D. C., AND C. D. GORDON. 1935. The sequence and appearance, molt, and replacement of the juvenile remiges of some domestic birds. *Journal of Agricultural Research* 51:459–470.
- WINKER, K. 2012. The wretched riddle of reduced rectrices in wrens. *Western Birds* 43:255–258.
- WRIGHT, T. F., E. E. SCHIRTZINGER, T. MATSUMOTO, J. R. EBERHARD, G. R. GRAVES, J. J. SANCHEZ, S. CAPELLI, H. MÜLLER, J. SCHARPEGGE, G. K. CHAMBERS, AND R. C. FLEISCHER. 2008. A multi-locus molecular phylogeny of the parrots (Psittaciformes): support for a Gondwanan origin during the Cretaceous. *Molecular Biology and Evolution*. 25:2141–2156.
- WYNDHAM, E. 1981. Molt of the Budgerigar *Melopsittacus undulatus*. *Ibis* 123:145–157.