

TWO MODES OF PRIMARY REPLACEMENT DURING PREBASIC MOLT OF RUFOUS FANTAILS, *RHIPIDURA RUFIFRONS*

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ABSTRACT.—We documented unusual variation in the sequence of primary replacement during the prebasic molt of Rufous Fantails (*Rhipidura rufifrons*) captured in 2009 and 2010 on Saipan, Northern Marianas Islands. Most captures (62%) followed a typical replacement sequence, starting at the proximal primary (P 1) and proceeding distally to the outermost primary (P 10), but some individuals (38%) commenced molt from medial feathers, either P 2, P 3, or P 4 with replacement proceeding bidirectionally from the point of origin in multiple molt series. The distribution of centers for medial origin was P 2 (3%), P 3 (77%), P 3 and/or P 4 (12%), and P 4 (8%), indicating this pattern was distinct from the typical (P 1) pattern and the commencement point was not fixed to a specific primary. Females and individuals undergoing the second prebasic molt were more likely to have a center among primaries 2–4 than males and older birds. Two females that showed a center at P 1 during molt in 2009 showed a center at P 3 or P 4 during molt in 2010 represented exceptions to this finding but also indicated the starting point could vary inter-annually in an individual. Multiple molt series among primaries are poorly documented in passerines and we provide the first evidence for this molting strategy in the Rhipiduridae. Our results suggest a molt center among primaries 2–4 in younger and female Rufous Fantails may have evolved to enable more-rapid replacement of primaries while maintaining better foraging ability among selectively disadvantaged individuals. Received 20 January 2012. Accepted 11 May 2012.

Molt sequence among primaries of passerine birds is largely fixed, replacement beginning with a center at the innermost primary (P 1) and proceeding distally in a single series to the outermost feather (P 9 or P 10). Preformative molt can be incomplete and eccentric in some species with molt commencing at a primary other than P 1, but replacement continues to be distal and in sequence (Pyle 1997). Multiple molt centers or series among primaries have been documented widely among non-passerine families including albatrosses (Diomedidae), alcids (Alcidae), falcons (Falconidae), parrots (Psittacidae), and owls (Strigidae) (Miller 1941; Langston and Rohwer 1995; Pyle 1997, 2008; Thompson and Kitaysky 2004), but only a few exceptions to distal and sequential replacement during complete prebasic molts have been documented in north-temperate passerines. The primaries of Spotted Flycatchers (*Muscicapa striata*; Muscicapidae) are replaced proximally (generally from P 10 to P 1) and, in a few European shrikes (Laniidae) and warblers (Lucostellidae), primary molt can begin with medial primaries and proceed bidirectionally, displaying multiple molt series (Cramp 1992, Cramp and Perrins 1993, Jenni and Winkler 1994). American Dippers (*Cinclus mexicanus*; Cinclidae), among North American passerines, have been reported to molt primaries out of

sequence commencing with a block of medial feathers (Sullivan 1965). We are unaware of other North American or tropical passerines that diverge from a single distal replacement series. Multiple molt series are thought to be an adaptation for increased foraging efficiency in birds with time constraints for molting (Tucker 1991, Hedenström and Sunada 1999, Pyle 2005, Rohwer et al. 2009); documentation of exceptions within families may lead to a better understanding of remigial-replacement strategies (Rohwer 1999).

Rufous Fantails (*Rhipidura rufifrons*; Rhipiduridae) occur in Australia, Indonesia, and islands of the southwestern Pacific Basin (Higgins et al. 2006). This passerine species is insectivorous with short rounded wings and relies heavily on aerial foraging strategies. We discovered some Rufous Fantails molting bidirectionally from a center among primaries 2, 3, or 4 during research on the demography of landbirds on Saipan, Northern Marianas Islands (Radley et al. 2011). Other individuals displayed a sequence more typical of passerines, commencing with P 1 and proceeding distally to P 10. Our objective is to document variation in the primary replacement sequence of Rufous Fantails on Saipan and discuss its possible evolutionary implications.

METHODS

Six mist-netting stations were operated from 11 April to 15 July 2009 and 21 February to 9

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TABLE 1. Molt patterns of Rufous Fantails captured in 2009 and 2010 at TMAPS stations on Saipan. Younger (SCB) individuals and females were more likely to have a primary 2–4 strategy than older (DCB) individuals and males.

	<i>n</i>	DCB ^{a,b}	SCB ^{b,c}	Males ^b	Females ^b
Primary 1 group	108	54	34	20	5
Primary 2–4 group	66	8	32	8	14
Primary 2 ^d	2	0	1	1	1
Primary 3 ^d	51	6	26	7	11
Primary 3/4 ^d	8	1	2	0	1
Primary 4 ^d	5	1	3	0	1

^a DCB (Definitive Cycle Basic) individuals are those undergoing at least their third prebasic molt.

^b Age and gender could not be ascertained for all captures.

^c SCB (Second Cycle Basic) individuals are those undergoing their second prebasic molt.

^d Values for P 2, P 3, P 3/4, and P 4 represent subsets of the primary 2–4 group.

October 2010 on Saipan (15° 12' N, 145° 45' E), a tropical Pacific island in the Northern Mariana Archipelago (Radley et al. 2011). Each mist-netting station was operated for 6 hrs once every 10 days following protocols established by the Institute for Bird Populations (DeSante et al. 2009). All unbanded birds were individually marked with numbered aluminum leg bands and many were classified to age and gender (Pyle et al. 2008, Radley et al. 2011). Wing chord was measured (± 1.0 mm) as unflattened right wing from wrist to tip of the longest primary. Mass (± 0.1 g) was measured using a digital scale. Rufous Fantails typically have a partial preformative molt and do not replace primaries or secondaries until the second prebasic molt. Age was assigned based on extent of skull pneumatization, plumage, and molt-limit criteria (Radley et al. 2011), and verified through recapture data when available. Age codes were defined based on plumage cycle (Wolfe et al. 2010) and birds were categorized as either second-cycle basic (SCB), including those undergoing the second prebasic molt, or definitive-cycle basic (DCB), including those undergoing the third or later prebasic molt. Individuals in breeding condition were assigned as male by the presence of cloacal protuberance or female by presence of a brood patch (Pyle 1997, Radley et al. 2011).

The presence or absence of symmetrical flight-feather molt was recorded for all birds captured. Both wings were scored for most captures to confirm sequence and assess symmetry between wings. We categorized individuals based on molt-score patterns (using the strategies of Rohwer 2008) as either showing distal sequential molt from P 1 (primary-1 group), showing molt centers at P 2, P 3, P 3/4, or P 4 and both distal and proximal replacement (primary 2–4 group), or

showing distal molt between P 5 and P 10 (primary 5–10 group). A center at P 3/4 was assigned when these two growing primaries were equal in length, indicating molt had commenced with both feathers at about the same time. Replacement of primaries 1–3 can be rapid and close to synchronous in passerines (Pyle 1997), and we were careful to ensure that P 1 was fresher than P 2 (and thus replaced earlier) in those categorized into the primary-1 group and in which both of these primaries were fully grown. We did not identify commencement point among primaries 1 to 4 in the primary 5–10 group and these birds are not considered further.

RESULTS

We captured 1,086 Rufous Fantails a combined 1,728 times during 2009 and 2010; 306 individuals were captured a combined 448 times when primaries were molting, and we scored primaries for 343 captures. Molt center and sequence among primaries 1–4 were categorized during 174 molt episodes for 166 birds (8 birds were scored twice during prebasic molt episodes in both 2009 and 2010). All documented molt sequences were symmetrical between wings within one full-grown feather, and no birds had varying molt centers on different wings.

Sequential replacement from P 1 was recorded for 108 of 174 molt episodes (62%) and a center among primaries 2–4 from which molt proceeded bi-directionally was recorded for the remaining 66 (38%) episodes (Tables 1, 2; Fig. 1). Most birds in the primary 2–4 group (77%) initiated molt at primary 3 (Table 1), and the distribution among centers (including 3% at P 2, 12% at P 3/4, and 8% at P 4) was normal (Kolmogorov-Smirnov test for normality: $D = 0.042$, $P > 0.15$). The mean starting point within this group was 3.11, or just

TABLE 2. Examples of feather scores for primary molt sequence of Rufous Fantails based on individuals captured on Saipan in 2009 and 2010 (following Rohwer 2008). Two examples of each primary center are shown. Numeric values represent proportion of feather growth; notations are Nodal (N) and Terminal (T), and arrows above notations indicate sequence direction.

Primary center	Primary									
	1	2	3	4	5	6	7	8	9	10
1	N0.3	0.2	→0.1	OLD	OLD	OLD	OLD	OLD	OLD	OLD
1	NNEW	→0.7	→0.4	→0.1	OLD	OLD	OLD	OLD	OLD	OLD
2	T←0.6	NNEW	OLD	OLD	OLD	OLD	OLD	OLD	OLD	OLD
2	T←0.2	N0.6	OLD	OLD	OLD	OLD	OLD	OLD	OLD	OLD
3	T←0.1	0.7	N0.8	0.6	→0.1	OLD	OLD	OLD	OLD	OLD
3	T←0.3	0.7	NNEW	0.8	0.4	→0.1	OLD	OLD	OLD	OLD
3/4	OLD	OLD	N0.2	N0.2	OLD	OLD	OLD	OLD	OLD	OLD
3/4	OLD	←0.5	N0.8	N0.8	→0.6	→0.1	OLD	OLD	OLD	OLD
4	T←0.3	0.5	←0.6	N0.7	0.4	0.1	OLD	OLD	OLD	OLD
4	T←0.1	0.3	←0.7	NNEW	0.6	0.1	OLD	OLD	OLD	OLD

distal to P 3, when calculated according to primary center number (P 3/4 scoring 3.5).

Younger (SCB) birds were more likely to initiate primary molt among primaries 2–4 than older (DCB) birds with a mean starting point of 2.01 versus 1.54 for older birds (ANOVA, $F_{2,183} = 4.03$, $P = 0.019$). Females (mean starting point 2.22) were more likely to initiate primary molt at primaries 2–4 than males (mean starting point 1.48; $F_{2,183} = 8.30$, $P = 0.006$; Table 1). Mean (\pm SE) wing chord among 31 males of our sample

was 67.1 ± 1.41 and mean wing chord among 22 females was 63.9 ± 1.73 mm ($F_{1,51} = 57.32$, $P = 0.000$). Mean mass among 29 males was 8.4 ± 0.43 g and mean mass among 22 females was 7.9 ± 0.37 g, ($F_{1,49} = 14.44$, $P = 0.000$). Wing chord was also significantly longer among 81 DCB birds (65.9 ± 1.96 mm) than among 62 SCB birds (64.7 ± 2.42 mm; $F_{1,140} = 5.62$, $P = 0.004$), but mass did not differ with age among 79 DCB (8.1 ± 0.47 g) and 62 SCB (8.0 ± 0.45 g) birds ($F_{1,140} = 1.55$, $P = 0.216$). The effects of age ($P = 0.052$)

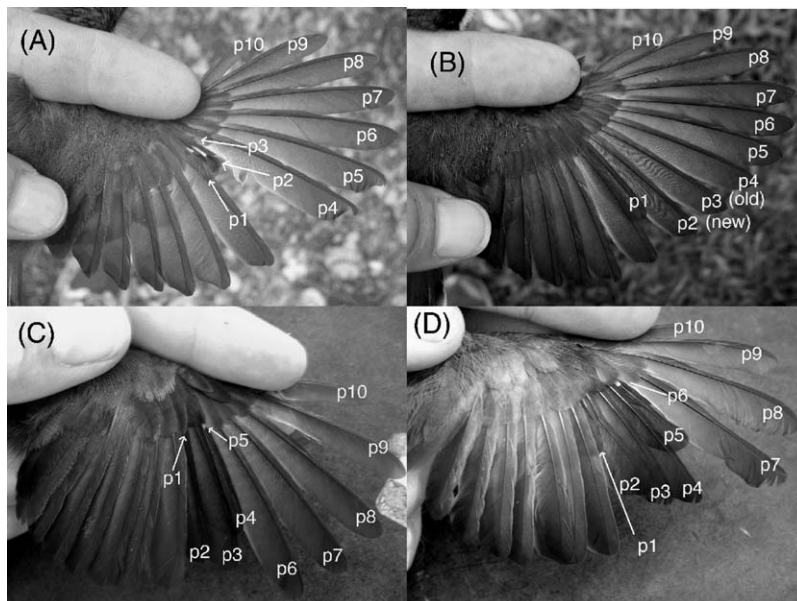


FIG. 1. Replacement patterns in Rufous Fantails captured on Saipan in 2009–2010. Primaries are numbered distally from P 1 (innermost) to P 10 (outermost). Images show centers at P 1 (A), P 2 (B), P 3 (C), and P 4 (D).

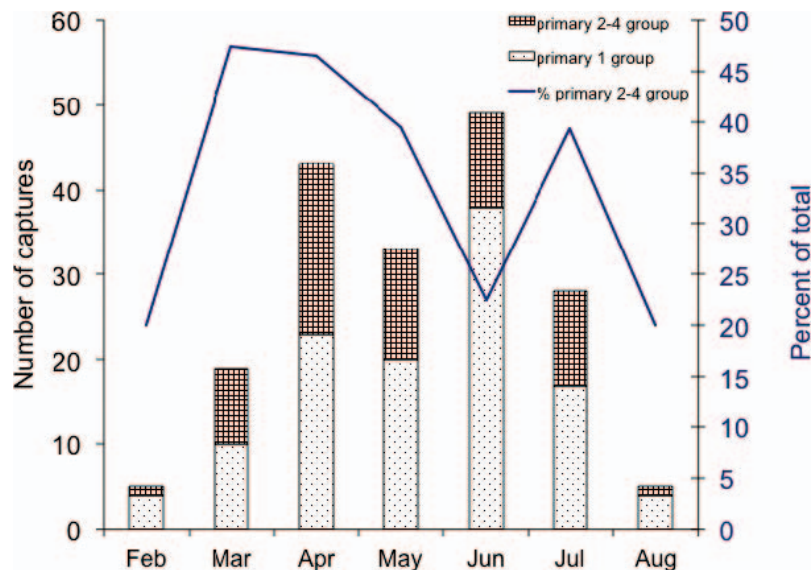


FIG. 2. Number of individual Rufous Fantails captured on Saipan showing centers at P 1 (bar stippling) and primaries 2–4 (bar hatching), and proportion of individuals with centers at primary 2–4 (line) by month during February to August 2009–2010.

and gender ($P = 0.038$) remained significant or nearly so, but the effects of wing chord ($P = 0.170$) and mass ($P = 0.828$) were not significant when analyzed using multiple ANOVA ($F_{2,47}$).

The within-month proportion of individuals captured in February to August that exhibited a center among primaries 2–4 varied from 20 to 47% with little evident seasonality (Fig. 2). Six of eight birds captured during separate prebasic molt episodes had the typical sequence from P 1 during both episodes, one DCB female had a center at P 1 in 2009 and a center at P 4 in 2010, and one SCB female had a center at P 1 in 2009 and a center at P 3 in 2010; these two individuals represented exceptions to the age-specific pattern.

DISCUSSION

Multiple molt centers or series among primaries are poorly documented in passerines and our results indicating a center at primaries 2, 3, or 4 for some Rufous Fantails provides the first evidence for multiple molt series in the Rhipiduridae (Higgins et al. 2006). The only North American passerine with an atypical primary molt sequence may be the American Dipper, where primaries 2–6 may drop simultaneously before P 1, an adaptation enabling rapid molt and resulting in brief flightlessness (Sullivan 1965). This should be confirmed, however, because the well-studied

White-throated Dipper (*Cinclus cinclus*) reportedly molts rapidly, but in typical sequence from P 1 (Cramp 1988).

The distribution of molt centers among the primary 2–4 group of Rufous Fantails with only 3% initiating molt at P 2 and the remainder showing a normal distribution, suggests this group exhibits a different mechanism affecting replacement sequence from the primary-1 group, rather than the center simply drifting among P 1 and P 4. The mechanism affecting center resulted in an average initiation point just distal to P 3 among our sample of individuals with medial molt centers. Some individuals appeared to have molted primaries 3 and 4 at or near the same time, suggesting the molt center may not be fixed at an individual primary, but can occur between two primaries or along a defined area along the alar tract. Fluidity in both molt commencement point and directionality has not been fully documented to our knowledge, although it appears to occur in Savi's Warblers (*Locustella luscinioides*; Jenni and Winkler 1994). Passerines with eccentric preformative molts among primaries can vary their center of initiation but distal sequence is maintained (Pyle 1997).

Mechanisms affecting molt strategies in birds remain poorly known due to complex interactions between physiological, environmental, and genet-

ic factors (Payne 1972); remigial molt sequence may be based on either neurophysiological events (Voitkevich 1966, Rohwer et al. 2011) or an endocrinological mechanism (Miller 1941, Bridge 2011). That two Rufous Fantails in our study switched from a center at P 1 during one molt episode to a center at P 3 or P 4 during the next episode suggests the sequence may be phenotypically plastic and adaptive based on environmental as well as genetic factors.

Regular molt centers other than P 1 have been documented among Eurasian passerines, most thoroughly for Brown Shrikes (*Lanius cristatus*; Stresemann and Stresemann 1971, Cramp and Perrins 1993) and Savi's Warblers (Thomas 1977, Cramp 1992, Neto and Gosler 2006); a few other individual cases in other passerine species have been reported (Jenni and Winkler 1994, Thompson and Kitaysky 2004), possibly representing anomalies or based on injuries. Most Brown Shrikes appear to have a center between primaries 4 and 5 (molt proceeding both distally and proximally), but some have either a single or a second center at primary 1. Other *Lanius* shrikes appear to have a normal distal sequence from P 1 in all individuals (Cramp and Perrins 1993). Commencement of primary replacement can be variable in Savi's Warblers with some birds having a distal sequence from P 1 and others appearing to have centers among primaries 2 and 6; birds initiating the prebasic molt at P 1 tended to commence molt earlier than those initiating molt among primaries 2–6 (Neto and Gosler 2006).

Rufous Fantails with molt centers among primaries 2–4 showed no apparent seasonal pattern within our capture periods (Feb–Aug). However, a complete assessment of seasonality would have to account for annual breeding phenology (which appears to vary between years; P. Radley and J. F. Saracco, pers. comm.) as well as age and gender variation in timing of molt; we currently lack the data to address this question. The greater proportion of younger (SCB) and female Rufous Fantails with a medial molt center compared to older birds and males suggests they may have a selective advantage in foraging that affects the molt commencement point. Neto and Gosler (2006) did not separate younger from older individuals in their study; similar age-specificity suggesting slower or later molts in younger birds could indirectly explain the tendency for medial molt centers to occur with later-molting Savi's Warblers.

Multiple series in larger birds, constrained from replacing all primaries in a single molting season, allows more feathers to be replaced in a shorter period without creating large gaps in the wing, thereby maintaining wing-surface integrity and greater ability to fly and forage (Tucker 1991, Hedenström and Sunada 1999, Rohwer 1999, Pyle 2005). Our results suggest a center among primaries 2–4 in younger and female Rufous Fantails may have evolved as an alternate strategy in groups with a selective foraging disadvantage to enable them to replace more primaries more rapidly while maintaining better foraging ability. However, direct correlation with wing loading (mass and wing chord) was not evident in our study after controlling for effects of age and gender.

It may be advantageous for younger and female fantails to have multiple molt series if they are under greater time or energetic constraints due to poorer foraging ability or greater breeding constraints, respectively. Females may initiate molt later than males on average because males abandon their broods and mates in favor of early molting (Svensson and Nilsson 1997, Hemborg and Merila 1998); this could result in the need for more rapid molting in breeding female fantails, perhaps varying regularly on an inter-annual basis. Rapid molt may be unusual in tropical climates, where time constraints are less severe than in temperate climates (Ryder and Wolfe 2009). Our results suggest an adaptation for rapid replacement in some short-winged passerines that rely on flight to forage for aerial insects, such as Rufous Fantails (Higgins et al. 2006).

Molt sequence among inner primaries is difficult to document unless specifically looked for because molt among inner primaries is rapid and few specimens have been collected at this stage (Pyle 1997). It is possible multiple series may occur more often than suspected among passerines. Molt sequence is especially poorly documented in tropical passerines (Ryder and Wolfe 2009), and discovery of additional tropical passerines with multiple molt series may shed further light on the evolution and adaptation of this strategy. We encourage further study to document molt sequence among inner primaries of passerines, and to investigate evolutionary causes for variation within and among species.

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