The Wilson Journal of Ornithology 128(1):56–69, 2016

MOLT PATTERNS, AGE CRITERIA, AND MOLT-BREEDING DYNAMICS IN AMERICAN SAMOAN LANDBIRDS

PETER PYLE,[1,5] KEEGAN TRANQUILLO,[2] KIMIKO KAYANO,[3] AND NICOLE ARCILLA[3,4]

ABSTRACT.—We examined 135 specimens and analyzed 1,735 captures of indigenous American Samoan landbirds, of nine target species in seven families, to document molt patterns, assess the extent of molt-breeding overlap, and present criteria to determine age. Preformative molts varied from absent to complete, and there was no confirmed evidence for prealternate molts. Molt strategies, age-determination criteria, and remigial replacement sequences were largely consistent with those of other temperate and tropical bird species within the same families. Suspended and/or arrested molts were recorded in seven species and staffelmauser or stepwise molt in two species, including the first report in a passerine. Our data suggest that staffelmauser and suspension of molt in passerines may share a common underlying mechanism. Despite broad overlap of breeding and molting seasons at the population level, we observed little evidence of molt-breeding overlap at the individual level. We suggest that molt and accompanying restoration processes may take precedence over breeding, as indicated by well-defined molting seasons despite apparent year-round or bi-modal breeding in some of our species. Tropical landbird species appear to be capable of suspending molt to breed when environmental conditions shift to facilitate successful reproduction. *Received 5 February 2015. Accepted 26 July 2015.*

Key words: age criteria, American Samoa, landbird, molt sequence, molt suspension, staffelmauser.

Molt strategies in tropical landbirds remain poorly known (Ryder and Wolfe 2009, Wolfe and Pyle 2012) despite some recent descriptions of molt patterns in certain tropical avifaunas or families (e.g., Pyle et al. 2004, Wolfe et al. 2009). In the tropical and subtropical Pacific Basin, molt patterns and age-determination criteria have only been described for a few endemic Hawaiian landbird species and those species breeding on Saipan, Northern Marianas Islands (Freed and Cann 2009, Radley et al. 2011). Breeding in tropical areas can occur year-round or can respond opportunistically to aseasonal interannual rainfall patterns, which in turn can result in more-complex molting regimes than are found in species that breed during succinct seasons in temperate or boreal regions. Molts in tropical areas, for example, may include an increased incidence of molt-breeding overlap or suspension of molt for breeding (Radley et al. 2011, Freed and Cann 2012, Johnson et al. 2012). Data on molting patterns from additional tropical regions are needed to better understand complex interactions between molting and breeding regimes.

In 2012, the Institute for Bird Populations (IBP) initiated a Tropical Monitoring Avian Productivity and Survivorship (TMAPS) program in American Samoa, where practically nothing was known of molt and breeding patterns or age-determination criteria for landbirds. Similar to the North American MAPS program, TMAPS utilizes data collected on captured landbirds at mist-netting stations to understand demographic parameters useful in implementing habitat conservation and management strategies (DeSante et al. 1995, Saracco et al. 2012). Accurate categorization of age, which relies on molt strategies and plumage development, is necessary to estimate vital rates and population demography using TMAPS data. Therefore, we initially operated TMAPS stations every month from August 2012 to August 2013, in order to assess breeding seasonality, molt patterns, and age-determination criteria throughout each species' complete annual cycle. Based on these data, we identified peak breeding and molting seasons and identified November–March as the optimal TMAPS period to capture the breeding season of most landbirds in American Samoa (Pyle et al. 2014). Here, we present molting strategies and age and sex criteria for nine landbird species indigenous to American Samoa (Table 1), and we assess the extent to which each species overlaps or separates breeding periods from those of the annual prebasic molt.

METHODS

A total of 16 TMAPS stations were operated on Tutuila (14° 17′ S, 170° 41′ W) and Ta'u (14° 14′ S, 169° 28′ W) islands, American Samoa, during all or

---

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

[2] P.O. Box 181, Virginville, PA 19564, USA.

[3] Department of Marine and Wildlife Resources, P.O. Box 3730, Pago Pago, American Samoa 96799.

[4] Current address: Department of Biodiversity, Earth and Environmental Science, Drexel University, Philadelphia PA 19104, USA.

[5] Corresponding author; e-mail: ppyle@birdpop.org

TABLE 1. Molt extents and WRP groupings for nine native Samoan landbird species.

		Molt extent		
Common name	Scientific name	Preformative	Prebasic	WRP group[1]
Purple-capped Fruit-Dove (PCFD)	*Ptilinopus porphyraceus*	Incomplete to Complete	Incomplete to Complete	1
Blue-crowned Lory (BCLO)	*Vini australis*	Partial	Complete	2
White-rumped Swiftlet (WRSW)	*Aerodramus spodiopygia*	Partial	Incomplete to Complete	3
Collared Kingfisher (COLK)	*Todiramphus chloris*	Absent	Complete	4
Samoan Shrikebill (SASH)	*Clytorhynchus powelli*[2]	Partial	Incomplete to Complete	3
Cardinal Honeyeater (CAHO)	*Myzomela cardinalis*	Incomplete	Incomplete to Complete	3
Wattled Honeyeater (WAHO)	*Foulehaio carunculata*	Partial	Incomplete to Complete	3
Samoan Starling (SAST)	*Aplonis atrifusca*	Partial	Incomplete to Complete	3
Polynesian Starling (POST)	*Aplonis tabuensis*	Partial	Complete	2

[1] WRP Groups have specific combinations of acceptable WRP age codes (see text and Johnson et al. 2011 for abbreviations): Group 1 = FCJ, FPF, FCF, SPB, FAJ, UPB, DCB, DPB; Group 2 = FCJ, FPF, FCF, SPB, UPB, DCB, DPB; Group 3 = FCJ, SPB, UPB, DCB, DPB; Group 4 = FCJ, SPB, SCB, TPB, UPB, DCB, DPB, SAB. All groups also have additional acceptable "unknown codes" (UPU, UCU, and UUU) which should be avoided if possible (see text).

[2] Samoan Shrikebill is split from Fiji Shrikebill (*C. vitensis*) following Pratt (2010).

parts of August 2012–August 2013, December 2013–March 2014, and December 2014–March 2015. Each station consisted of 10 mist nets operated for ~6 hrs per day, for up to 3 consecutive days (a "pulse"), once per month, following IBP protocols for stations in tropical regions (DeSante et al. 2005). On Tutuila, six stations were operated during most of the above months, although four stations had to be discontinued and replaced by other stations in 2012 or early 2013 because of poor capture rates or logistical considerations. Twelve stations (six on Tutuila and six on Ta'u) were then operated monthly during December 2013–March 2014 and December 2014–March 2015. For each captured or recaptured bird, complete data were obtained according to MAPS protocols (DeSante et al. 2012), and wing chord, tail, and bill measures were obtained following the methods of Pyle (1997). Most captured birds were photographed, including images of body, spread-wing, and spread-tail, to confirm age and molting status.

Molt patterns and criteria to determine age and sex were developed initially based on examination of specimens by PP (see Acknowledgments for collection locations) along with a synthesis of information from the literature on American Samoan and other congeneric species (Mayr 1933, 1941, 1942; Amadon 1942, 1943a,b; Banks 1984; Higgins 1999; Higgins et al. 2001, 2006; Radley et al. 2011). Each specimen was evaluated for molting status, extent of previous molts, age, and sex (as supplemented by information on specimen labels), and wing chord and other measures were obtained following methods of Pyle (1997). A preliminary manual was developed (Pyle 2013b) based on these specimen data that was then updated and refined based on the first year of capture data collection.

To classify birds to age, we used the "WRP" age-coding system (Wolfe et al. 2010, Johnson et al. 2011) developed for use in tropical regions, where calendar-based age-coding is impractical. The WRP system codes age-groups according to molt cycles and plumages following the terminology of Humphrey and Parkes (1959) and Howell et al. (2003). WRP age codes indicate whether or not a bird is actively molting and categorizes plumages based on the previous prebasic or inserted molts. WRP codes used here include: first cycle, juvenile plumage (FCJ); first cycle, undergoing the preformative molt (FPF); first cycle, formative plumage (FPF); plumage after (older than) juvenile (FAJ); second cycle, undergoing the second prebasic molt (SPB); second cycle, basic plumage (SCB); third cycle, undergoing the third prebasic molt (TPB); definitive cycle, basic plumage (DCB); definitive cycle, undergoing the definitive prebasic molt (DPB); and after (older than) second cycle (SAB); see Johnson et al. (2011) and Pyle et al. (2015) for tables summarizing these codes. Additional age categories and codes, indicating unknown molt and/or plumage status, were used occasionally; these include non-molting individuals of unknown cycle and plumage (UCU), individuals undergoing an unknown molt (UPU), individuals undergoing either the second or definitive prebasic molt (UPB), and individuals of unknown molt and plumage status (UUU). These unknown codes were used when age and/or molt status could not be determined, often as a result of escape prior to all data being recorded; UPB was also used for birds just completing final feather growth of either the second or definitive prebasic molt. Depending on extents of the preformative and definitive prebasic molts in a species, acceptable WRP codes were derived for each species (Table 1; see also Pyle et al. 2015).

Primaries were numbered from innermost (p1) to outermost (p10), tertials were numbered from innermost (t1) to outermost (t3), other secondaries were numbered from outermost (s1) to innermost (s6, s7, or s8, depending on the species), and rectrices were numbered from innermost (r1) to outermost (r5 or r6, depending on the species) on each side of the tail. For birds captured at TMAPS stations, data on the progress and sequence of active flight-feather molt were obtained following the recommendations of Rohwer (2008). Each primary was scored as new (10), missing (1), growing (scored 1–9 to the nearest 10% of full growth), or old (0), resulting in active molt scores between 1 (one primary dropped) and 100 (primary molt completed and secondary molt completing), and these scores were used to indicate overall molt progress. These data were also used to determine precise molt sequence, including initiation (nodes) and completion (termini) points, among primaries, tertials, and adjacent secondaries. Non-molting birds that had suspended or arrested molt of primaries or secondaries were also scored.

We considered captured birds as actively breeding if either a brood patch or a cloacal protuberance (Pyle 1997) was scored as "partial" or "full" following DeSante et al. (2012; scores 2 or 3). Recaptures of the same individual from separate pulses were included in analyses of molt and breeding seasonality, but only the first capture of an individual within a pulse was included. Measurement data were included only from the first capture of an individual.

RESULTS

Our analyses included a total of 135 specimens and 1,735 captures of our nine target species (Table 1). Of the 1,735 captures, 535 (31%) were of birds undergoing active remigial (primary and/or secondary) molt and 231 (13%) were of individuals in active breeding condition. All nine species have 10 primaries. Unless otherwise indicated, prebasic or preformative molt sequence progressed from a node at the innermost (p1) to a terminus at the outermost (p10) primary, and sequence among secondaries proceeded from a node at either the innermost tertial (t1) distally or the second tertial (t2) bilaterally, followed by a node at the outermost secondary (s1) proximally. The terminal secondary replaced in most species was either s6 or s5. None of our study species showed evidence confirming prealternate molts, so acceptable age determination and coding was based on extents of preformative molts in the first cycle and prebasic molts in second and definitive cycles. Four species groups were identified according to molting patterns and acceptable WRP coding choices (Table 1; see also Pyle et al. 2015).

The following accounts summarize molt, breeding status, and age-determination criteria for each species. Measurement ranges (mm) from the literature (cited above), specimens, and captured birds combined, are present based on mean ± 2*SD, to eliminate outliers and to represent ~95% of the sample (see Pyle 1997). Age criteria common to all species include narrower and more tapered juvenile primaries and rectrices in FCJs and FCFs (of species with incomplete preformative molts) than in DCBs and older age groups (Pyle 1997), and molt clines among the secondaries in DCBs but not FCFs of species with incomplete preformative molts (Pyle 2008), reflecting previous protracted replacement as is typical in tropical passerines.

Species Accounts

Purple-capped Fruit Dove.—(Ptilinopus porphyraceus; $n = 19$ specimens and 36 captures). Both the preformative and the definitive prebasic molts can be incomplete or complete, resulting in acceptable WRP codes for species Group 1 (Table 1). Active preformative ($n = 8$) and prebasic ($n = 9$) molts were recorded throughout the year (all months except Apr, Aug, and Sept), without any apparent seasonal peaks in timing. Secondaries were recorded molting proximally from nodes at s5 as well as s1 (Table 2B). One bird commenced tertial molt with t2 (Table 2A) whereas none showed evidence of distal replacement from t1. Evidence of staffelmauser or stepwise molt (Stresemann and Stresemann 1966, Pyle 2006) was recorded in 13 of 38 individuals (e.g., Table 2A, Fig. 1B). Only three birds were captured in breeding condition, in December, January, and March, and none of these were simultaneously undergoing active molt.

Juvenile (FCJ) Purple-capped Fruit-Doves lack purple caps, show pale-tipped upperpart feathers and remiges, and have blunter tips to the notched juvenile outer primaries than in subsequent

TABLE 2. Captures of American Samoan bird species showing variation in replacement sequences among secondaries and primaries.[1]

				Secondaries											Primaries									
	Species	Band	Date	t1	t2	t3	s8	s7	s6	s5	s4	s3	s2	s1	p1	p2	p3	p4	p5	p6	p7	p8	p9	p10
A	PCFD	085416900	8 Jan 13	O	N	O	O	O	O	O	8	O	N	O	N	7	O	O	O	N	N	N	3	O
B	PCFD	085416879	5 Jul 13	X	N	N	O	O	X	N	O	O	O	O	N	N	N	N	8	X	O	O	O	O
C	BCLO	135230494	7 Feb 14	N	N	N	-	O	9	N	N	7	2	O	O	7	N	N	S	N	N	N	8	X
D	COLK	135230006	8 Aug 12	N	N	N	N	N	5	O	9	N	N	N	N	N	N	N	N	N	N	N	N	8
E	COLK	135230146	17 Jun 13	N	N	N	N	N	N	5	3	N	N	N	N	N	N	N	N	N	N	N	N	6
F	SASH	184130506	9 Jan 14	O	7	2	-	-	O	O	O	O	O	O	7	4	X	O	O	O	O	O	O	O
G	SASH	184130572	22 Feb 14	O	8	X	-	-	O	O	O	O	O	O	X	6	5	1	O	O	O	O	O	O
H	SASH	184130591	3 Mar 14	O	7	3	-	-	O	O	O	O	O	O	1	8	4	X	O	O	O	O	O	O
I	SASH	184130509	29 Dec 14	N	N	N	-	-	O	O	N	N	N	N	N	N	N	N	N	N	N	N	O	O
J	CAHO	252158908	27 Feb 12	N	N	N	-	-	O	O	O	O	N	N	N	N	N	N	N	N	N	N	O	O
K	WAHO	256191605	22 Mar 13	N	N	N	-	-	9	6	N	N	N	N	N	N	N	N	N	N	N	N	9	7
L	WAHO	184130522	28 Dec 13	O	X	O	-	-	8	N	O	O	O	O	5	1	X	O	O	O	O	O	O	O
M	SAST	084423034	14 Dec 13	N	N	N	-	-	O	O	O	N	N	N	N	N	N	N	N	N	N	N	N	N

[1] See Table 1 for four-letter species codes and Rowher (2008) for presentation and interpretation of molt data; O = old feather, N = new feather, X = missing feather, and numbers represent tenths of a growing feather. A dash (-) indicates that this secondary is not present in the species. See text for discussion of each line of data.

plumages (Fig. 1). The highly modified formative or basic p10 likely results in acoustic signaling during aerial courtship. These juvenile plumage and primary-shape traits were also found in *P. roseicapilla* (Radley et al. 2011) and *P. perousii* (Pyle 2013b) and may be common to the genus *Ptilinopus*. Following complete molts, FCF is not distinguishable from DCB, and birds were aged FAJ. Individuals with retained juvenile primaries or secondaries, after suspended or

FIG. 1. Shapes of juvenile (left, band # 178375730 captured 19 Mar 2013) and basic (right, band # 085416872 captured 21 Jan 2013) outer primaries (p10) in Purple-capped Fruit-Dove to assist with age determinations. Note also the suspended molt between p7 and p8 on the right-hand image (B), part of a staffelmauser molting pattern, and allowing age-code assignment of DCB (see text).

arrested preformative molts, were aged SCB, and those with retained formative or basic feathers as part of staffelmauser patterns were aged DCB. Among post-juvenile birds, males can be distinguished from females by showing brighter and more-extensive magenta on the crown, bluer-tinged napes, and broader and more complete yellow tips to the rectrices. Sexes (both islands combined) differentiated moderately by wing chord: ♀ (n36) 124–137 and ♂ (n25) 132–146 mm, with FCJs and FCFs falling in the bottom portions of each range.

Blue-crowned Lory.—(Vini australis; *n* = 15 specimens and 14 captures). The preformative molt is partial, including body feathers but no wing or tail feathers, and the definitive prebasic molt is complete, resulting in acceptable WRP codes for species Group 2 (Table 1). Active prebasic molt was recorded in August–February to indicate a protracted molting season during this period; Banks (1984) also noted peak molting in December–January. Molting patterns indicated bilateral replacement from nodes at p5 and s5 and that molt could be suspended for breeding after p5 had been dropped (e.g., Table 2C). Suspension occasionally occurred elsewhere within remigial tracts; overall suspended molt was present in four of 15 SCB or older birds in which this could be assessed. A node at t2 was confirmed for one bird, whereas none showed a node at t1. No individuals were captured in breeding condition; based on gonadal development in collected specimens, Banks (1984) noted breeding condition in June but little to none in December–January, suggesting more-active breeding in February–November, followed by active molting.

Juvenile plumage (FCJ) is undescribed in Blue-crowned Lory, but it may have reduced extents of duller blue in the crown and red in the underparts, darker bill and eye color, and duller leg color, as in other parakeets of the genus *Vini* (Higgins 1999). Crown and underpart coloration averages duller in FCFs and females than in DCBs and males, but there is overlap among age/sex groups. Definitive outer primaries may have more distinct notches to the tips than juvenal outer primaries. These criteria and molt clines (Pyle 2013a) can be used to distinguish FCFs and DCBs, after which sex determination can be attempted by plumage brightness. Sexes of this species on Ta'u appear relatively monomorphic: wing chord ♀ (n23) 102–113, ♂ (n25) 104–117; tail length ♀ (n19) 61–67, ♂ (n19) 61–69 mm.

White-rumped Swiftlet.—(Aerodramus spodiopygia; *n* = 6 specimens and 18 captures). The preformative molt is partial, including body feathers but not wing feathers, and the prebasic molt is incomplete to complete, resulting in acceptable WRP codes for species Group 3 (Table 1). Two specimens captured in December had initiated prebasic molt, and two specimens collected in March and one capture in May were completing this molt, suggesting a molting season of November–May (see also Banks 1984). Three swifts captured in December had suspended the prebasic molt after p1–p3 (but no secondaries) had been replaced. This compares with nine DCBs showing evidence of complete uninterrupted molts. No individuals were captured in breeding condition but information from other specimens (Banks 1984) and our data suggest that breeding occurs during March–October, followed by molting.

Juvenile (FCJ) White-rumped Swiftlets show narrow buff fringes to upperpart feathers, secondaries, and inner primaries when fresh. There may also be molt limits visible between replaced scapulars and retained wing coverts in FCFs but not DCBs. SCB and SAB can be coded for birds that have suspended or arrested second or later prebasic molts, respectively. Insufficient data were available to assess sex-specific biometrics; 18 captures (both islands combined) of unknown sex had wing chord 107–120 and tail length 47–53 mm, with no evidence of a bimodal distribution suggesting sex-specific dimorphism.

Collared Kingfisher.—(Todiramphus chloris; *n* = 20 specimens and 206 captures). The preformative molt is absent and the definitive prebasic molt is complete, resulting in acceptable WRP codes for species Group 4 (Table 1). Ten individuals showed a node at t2 and in nine individuals t1 was nodal. The terminal secondary was either s5 (*n* = 3 captures), or s6 (*n* = 2; Table 2D–E). Active prebasic molt within the population commenced in December and completed in August (Fig. 2A). No evidence of suspended or incomplete molts was observed. None of our captures had developed brood patches or cloacal protuberances, but specimen evidence (Banks 1984) indicates peak gonadal activity in October–November, a period during which no birds were recorded molting (Fig. 2A).

As in Saipan (Radley et al. 2011), FCJ Collared Kingfishers show white fringing to the upperwing secondary coverts and thin dusky mottling to the breast when fresh. Females have darker to bright green backs and turquoise flight feathers and males

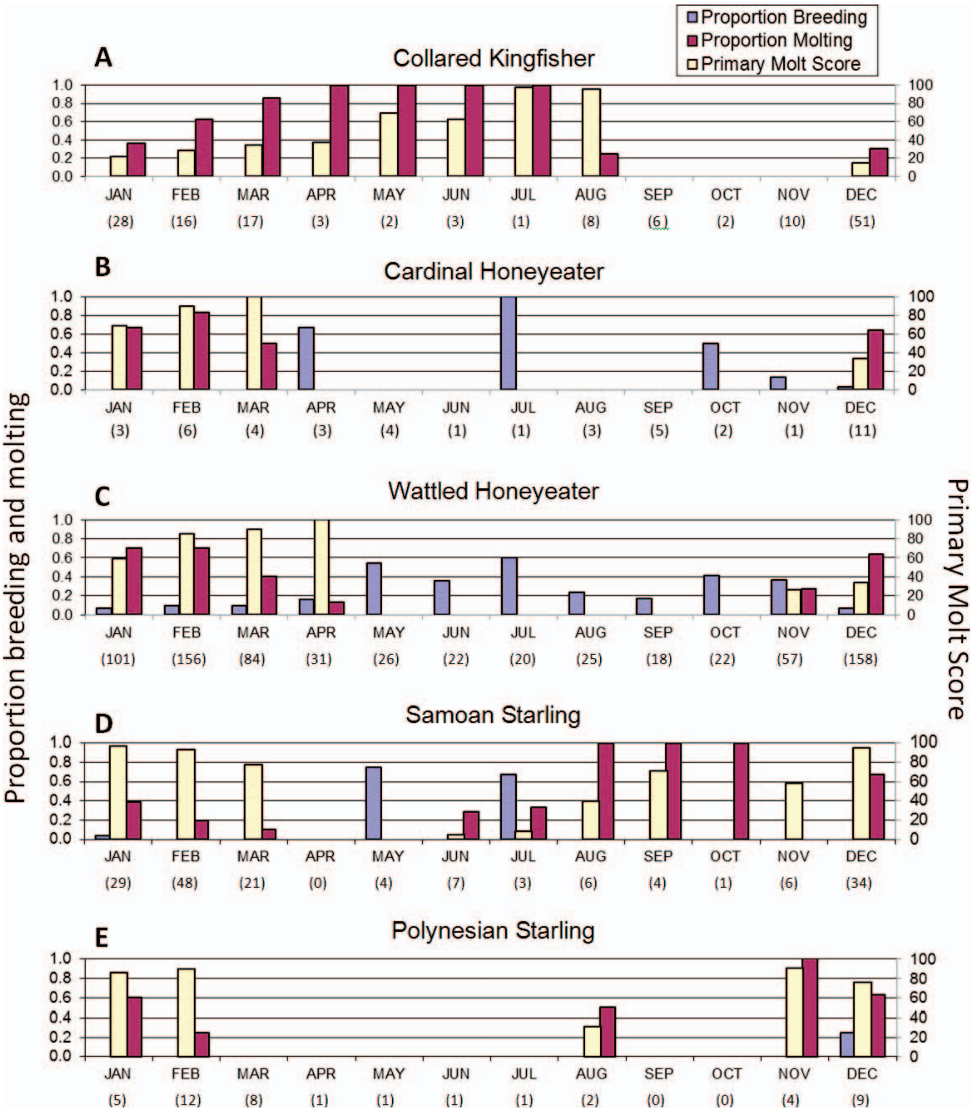

FIG. 2. Proportion of captured adult (SPB, SCB, DCB, DPB, UPB, or SAB; see text) individuals breeding and molting during each month, and mean primary replacement scores for birds in active molt, for five species of indigenous American Samoan landbirds. Sample sizes of captured birds are in parentheses below each month.

have turquoise to blue backs and pale to bright blue flight feathers, in both sexes averaging brighter and bluer in DCBs than in FCJs. Wing chord was not useful for sex determinations, averaging slightly larger in females than males and slightly larger on Ta'u than on Tutuila: ♀ (n88) 90–100 and ♂ (n129) 89–99 mm on Tutuila; ♀ (n40) 92–100 and male ♂ (n90) 91–99 mm on Ta'u.

Samoan Shrikebill.—(Clytorhynchus powelli; *n* = 10 specimens and 55 captures); we follow Pratt (2010) in considering Samoan Shrikebill a separate species from Fiji Shrikebill (*C. vitiensis*). The preformative molt is partial and the prebasic molt is incomplete to complete, resulting in acceptable WRP codes for species Group 3 (Table 1). The preformative molt includes body feathers and upperwing lesser coverts, most to all median coverts, and 1–6 inner greater coverts but no other wing or tail feathers. Nodes among the inner primaries varied, with typical sequence (p1 nodal) recorded for one DPB and two SPB individuals (e.g., Table 2F) and a node at p2 recorded for five

FIG. 3. Samoan Shrikebill (band # 184130591 captured 3 Mar 2014) showing a molt-commencement node at p2 as opposed to p1, with p1 and p4 dropped and p2 longer than p3 (primary scores for this bird are shown in Table 2H). Bilateral replacement from within the primary tract is rare in passerines (see text).

FIG. 4. Formative-plumage (FCF) Cardinal Honeyeater (band # 252158960 captured 23 Mar 2013) showing retention of inner 5 juvenile primary coverts. The browner and more-worn condition of these coverts allows age-determination; older individuals (DCBs) have uniform primary coverts and primaries.

individuals (three SPBs and two DPBs; e.g., Table 2G–H, Fig. 3). Among tertials, a node at t2 was recorded for 11 individuals (e.g., Table 2F–H), whereas no individual showed t1 nodal. In four captures s6 was terminal, although this feather was growing and only slightly shorter (by 0.1–0.2 feather lengths) than s5 on three of these captures. An actively breeding SAB female was captured that had suspended or arrested molt, retaining basic p9–p10 and s5–s6 on both wings (Table 2I) and a second SAB had retained the basic p10 on both wings; this compares with 26 DCBs that had undergone uninterrupted complete molts. Twenty of 38 birds captured in December–March were undergoing active prebasic molt, with molt generally commencing in December–January and completing in March or later, although two UPB individuals had nearly completed molt by mid-January. Mayr (1933) also assumed active molt occurred in January–April based on specimen evidence. Seven females and two males were captured in active breeding condition, all during December or early January, and none of which were simultaneously molting. These data indicate that breeding probably occurs primarily in November–January, followed by the prebasic molt.

Juvenile (FCJ) Samoan Shrikebills resemble birds in later plumages except for having rufous-fringed wing coverts. FCFs can be identified by thinner and more worn outer primaries and rectrices (see above) as well as molt limits in the upperwing coverts, the retained juvenile greater coverts fringed rufous when fresh, whereas DCBs have uniform and glossier wing coverts. SCB and SAB can be coded for birds that have suspended or arrested the second or later prebasic molts, respectively. Sexes are alike in plumage and differ only slightly in average wing chord length: ♀ (n16) 87–90 and ♂ (n12) 88–93 mm.

Cardinal Honeyeater.—(Myzomela cardinalis; *n* = 16 specimens and 106 captures). The preformative molt is incomplete and the prebasic molt is incomplete to complete, resulting in acceptable WRP codes for species Group 3 (Table 1). The preformative molt often includes all feathers except the inner 2–6 primary coverts (Fig. 4). Among tertials, a node at t2 occurred in 8 individuals, whereas no individual showed t1 nodal. During prebasic molts, s6 was terminal in 10 individuals and s5 in three individuals; during the preformative molt, s6 was terminal in five individuals and s5 in no individuals. At least five of 37 individuals showed evidence that the definitive prebasic molt had suspended or arrested before all primaries or secondaries had been replaced (e.g., Table 2J). Active prebasic molt within the population commenced in December and completed in March (Fig. 2B), whereas birds in active breeding condition were recorded in April to December, none of which were simultaneously in active molt. Body molt occurred more extensively around the year than in other Samoan landbirds, suggesting the possibility of a prealternate molt, although there was no indication of a distinct inserted molting season. Active preformative molt of primaries was recorded throughout the year, and molt scores

FIG. 5. Wattled Honeyeater (band # 121243359 captured 7 Jan 2014) with evidence of suspended molt; p3–p5 are new, following suspension after p1–p2 had been replaced, and suspending again after p5 had been replaced. The left wing showed a similar pattern except that p2–p5 had been replaced after and before suspensions. Outer primaries are basic so this bird was age-coded SAB.

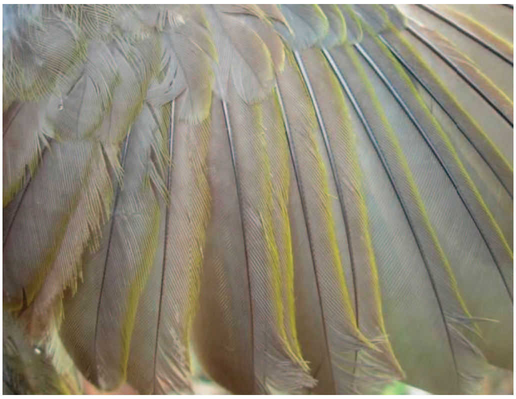

FIG. 6. Wattled Honeyeater (band # 184130549 captured 7 Feb 2014) with growing s5 and old s6, during commencement of a prebasic molt. This molt condition was symmetrical on both wings, and indicates that arrested feathers during one molt can be the first replaced in a subsequent molt in passerines, similar to staffelmauser molt patterns in non-passerines. Four other Wattled Honeyeaters (e.g., Table 2L) and two Samoan Starlings also showed this pattern.

indicated a pattern of protracted molt, many FPFs molting inner primaries in December–March and outer primaries in June–December.

Juvenile (FCJ) Cardinal Honeyeaters of both sexes show olive-gray to brown plumage without red feathering. DCB females have olive-fringed, gray body and wing feathers with incomplete reddish feathering in the head, back, rump, and uppertail coverts, and DCB males show bright red body plumage and black wings and tail. FCFs can be identified by having retained inner primary coverts which are browner than the remainder of the wing feathers (Fig. 4); FPFs and FCFs can be sexed by the color of formative feathers, gray and reddish in females or black and bright red in males. SCB and SAB can be coded for birds that have suspended or arrested the second or later prebasic molts, respectively. Wing chord is useful for sex determinations, averaging larger in males than in females on Tutuila: ♀ (n29) 55–64 and ♂ (n81) 62–72 mm, with FCJs and FCFs falling in the bottom portions of each range.

Wattled Honeyeater.—(Foulehaio carunculata; *n* = 11 specimens and 989 captures). The preformative molt is partial and the prebasic molt is incomplete to complete, resulting in acceptable WRP codes for species Group 3 (Table 1). The preformative molt includes body feathers and upperwing lesser coverts, most to all median coverts, no to all inner greater coverts, sometimes (during about 22% of preformative molts) 1–3 tertials, and occasionally (during about 5% of preformative molts) 1–6 central rectrices (among r1–r3). Among tertials, a node at t2 was recorded for 133 individuals (during 32 preformative molts and 101 prebasic molts), whereas 17 individuals (during four preformative molts and 13 prebasic molts) showed a node at t1, and among secondaries, s6 was terminal in 109 individuals, s5 was terminal in 10 individuals (e.g., Table 2K), and seven individuals had s5 and s6 growing at the same length. Thirty-nine individuals showed evidence of incomplete or suspended prebasic molts (e.g., Fig. 5; 10 second prebasic and 29 definitive prebasic molts), whereas 480 individuals lacked evidence of suspended or incomplete prebasic molts. Notably, 29 of these 39 individuals that had suspended molt were females (19 of which were actively breeding), four were of unknown sex, and only six individuals that had suspended or arrested molt were males. Four females and one male showed evidence that retained s5 and/or s6 from one molt could be among the first feathers replaced during the subsequent molt (Table 2L; Fig. 6).

A distinct molting season occurred within the population from November to April (according with the observations of Mayr 1933 and Banks 1984), whereas breeding appeared to occur at low levels throughout the year, with possible bimodal peaks in May–July and October–November (Fig. 2C).

Twenty-two actively breeding individuals were also undergoing active primary molt, representing 11.4% of actively breeding birds captured and 6.4% of individuals either actively breeding or molting. These birds had only partial brood patches (*n* = 5) or cloacal protuberances (*n* = 17) and primary molt scores either <12 or >89, indicating developing or receding reproductive conditions during completion or initiation of primary molt, respectively.

Juvenile (FCJ) Wattled Honeyeaters resemble birds in later plumages except for having more distinct pale edging to the wing coverts. FCFs were identified by molt limits in the upperwing coverts, and among the tertials and rectrices in some birds (see above), the retained juvenile feathers being contrastingly worn as compared with replaced formative feathers, whereas DCBs showed uniform, glossier and broader wing and tail feathers. SCB and SAB were coded for birds that had suspended or arrested the second or later prebasic molts, respectively. Sexes are alike in plumage, but our data indicate that all birds on both Tutuila and Ta'u can be sexed by wing chord: ♀ (n198) 85–95 and ♂ (n296) 96–107 mm, with no substantial difference in wing lengths between the two islands.

Samoan Starling.—(Aplonis atrifusca; *n* = 17 specimens and 245 captures). The preformative molt is partial and the prebasic molt is incomplete to complete, resulting in acceptable WRP codes for species Group 3 (Table 1). The preformative molt includes body feathers and upperwing lesser coverts, most to all median coverts, no to some inner greater coverts, and sometimes (during about 10% of preformative molts) 1–2 tertials (among s8–s9) and/or 1–4 central rectrices (r1–r2). The prebasic molt appeared to be protracted, beginning in June–August and completing in December–March (Fig. 2D). Seven individuals showed t2 nodal, whereas no individuals showed t1 nodal, and a terminus at s6 was observed in 34 individuals and one at s5 in nine individuals. Seventeen SAB and three SCB individuals showed evidence of incomplete or suspended prebasic molts (e.g., Table 2M), whereas 82 individuals lacked evidence of suspended or incomplete molts.

One SAB female and one SAB male showed evidence that retained s5 and/or s6 from one molt could be among the first feathers replaced during the subsequent molt, as noted for Wattled Honeyeater (see Table 2L; Fig. 6), and one DPB female was captured undergoing staffelmauser-like replacement of primaries, with p2 and p7 growing simultaneously on both wings (Fig. 7). Only six captured birds were in active breeding condition, one in January, three in May, and two in July (Fig. 2D), none of which were also undergoing active molt; however, an additional 11 adult females were captured with receding brood patches in November and early December. Our data along with those of Banks (1984) suggest a primary breeding season of May–November with lower-level breeding in December–April.

FIG. 7. Samoan Starling (band # 84423051 captured 27 Feb 2015) with growing p2 and p7 (symmetrically on both wings) and showing molt patterns among primaries and secondaries indicating staffelmauser or stepwise molt. Together with other Samoan Starlings as well as Wattled Honeyeaters that have begun prebasic molts with retained inner secondaries (e.g., s5 and s6; see Fig. 6, Table 2L), this suggests that staffelmauser in non-passerines and suspension for molt in passerines may share a common underlying mechanism.

Juvenile (FCJ) Samoan Starlings resemble birds in later plumages except body feathers and wing coverts are browner and upperpart feathers may have slightly wider pale fringing. FCFs were identified by molt limits in the upperwing coverts, and occasionally among the tertials and rectrices (see above), the retained juvenile feathers contrastingly brown and worn as compared with replaced formative feathers. DCBs showed uniform, glossier and broader wing and tail feathers. SCB and SAB were coded for birds that had suspended or arrested the second or later prebasic molts, respectively. The length of the reduced outer primary (p10) varied substantially, ranging from 4 mm shorter to 9 mm longer than the longest primary covert, but we found no relationship between length or shape of p10 and age, sex, or island of capture.

In FCFs and DCBs, males averaged glossier than females but there was substantial overlap between the age-sex groups in this character. In females, mean length of glossy tips was 6.0 for nape feathers (95% CI 4.3–7.6, $n = 39$), 4.8 for back feathers (3.1–6.3; $n = 30$), and 4.0 for breast feathers (2.3–5.5; $n = 31$), whereas respective values for males were 7.1 (5.5–8.7; $n = 36$), 5.3 (3.8–5.8; $n = 30$), and 5.1 (3.4–6.8; $n = 33$). Bill size was also larger in males (means: from nare to tip 22.2, depth at nare 10.4, and width at nare 9.3; $n = 59$–61) than in females (21.0, 9.7, and 8.8, respectively; $n = 57$–62) with ~50% overlap in each sex. Our data indicate that wing chord, however, could be used to sex all birds on each island: ♀ (n23) 132–142 and ♂ (n41) 145–154 mm on Tutuila; ♀ (n49) 136–145 and ♂ (n85) 148–157 mm on Ta'u.

Polynesian Starling.—(Aplonis tabuensis; $n =$ 21 specimens and 66 captures). The preformative molt is partial and the prebasic molt is complete, resulting in acceptable WRP codes for species Group 2 (Table 1). The preformative molt includes most to all body feathers and upperwing lesser coverts, some to most median coverts, no to some inner greater coverts, and rarely 1–2 tertials, but no other remiges or rectrices. A node at t2 was recorded for one individual, whereas no individuals showed a node at t1, and a terminus at s6 was shown by six individuals and a terminus at s5 in one individual. No individuals showed evidence of incomplete or suspended prebasic molts. Molting appeared to occur primarily in November–February. Only three captured birds were in active breeding condition, males in December with partial cloacal protuberances (Fig. 2E), none of which were undergoing active molt.

Polynesian Starlings differ in plumage by island. DCBs show blackish unstreaked underparts on Ta'u and dark gray underparts with pale streaks on Tutuila.

Juveniles (FCJs) show body plumage that is paler brown than FCFs, which are in turn browner than in DCBs. We also identified FCFs by molt limits between paler brown juvenile and darker brown formative upperwing coverts, whereas DCBs showed uniform, glossier and broader wing and tail feathers. Head plumage appeared to be glossier in DCBs than in FCFs and glossier in males than in females, but measurements of gloss tips did not differ by age and sex as in Samoan Starling (see above). As with Samoan Starling, the length of the outer primary varied, ranging from 3–11 mm shorter than the longest primary covert, but, as in Samoan Starling, we found no relationship between length or shape of p10 and age, sex, or island of capture. Bill dimensions also showed little or no variation between sexes, but our data indicate that wing chord could be used to sex all birds on each island: ♀ (n55) 99–106 and ♂ (n49) 107–115 mm; birds on Ta'u averaged slightly smaller than those on Tutuila, within the above ranges.

DISCUSSION

We present detailed molt strategies and criteria for determining age and sex in nine species of American Samoan birds, of seven avian families, and we assess the degree in which molt and breeding overlap in each. Preformative molts varied from absent in one species (Collared Kingfisher) to complete in one species (many Purple-capped Fruit-Doves), and there was no confirmed evidence for prealternate molts in any of the nine species. We present detailed information on molt sequences among primaries and secondaries, and document that a prebasic molt can commence with feathers retained from the previous prebasic molt, a staffelmauser-like pattern not previously documented in passerines. Otherwise, molt strategies and resulting age-determination criteria in these birds largely accord with patterns for other resident non-passerine and passerine landbirds in tropical areas and elsewhere (Pyle 1997; Higgins 1999; Higgins et al. 2001, 2006; Wolfe and Pyle 2012; Pyle et al. 2015).

Remigial Molt Sequences

In our nine target species, primaries were consistently replaced from the innermost (p1) to the outermost (p10), except in Blue-crowned Lory where molt proceeded bilaterally from a center at p5 as is typical in Psittaciformes (Pyle 2013a), and in some Samoan Shrikebills where molt commenced at p2 instead of p1 in five of eight individuals. Molt commencing from centers other than p1 is rare among passerines (Pyle 2013a), although commencement varying from p1 to p4 has been documented for Rufous Fantail *Rhipidura rufifrons* (Junda et al. 2012), another tropical Pacific flycatcher within or closely related to Monarchidae.

Among secondaries, sequence proceeded from the tertials distally and the outermost secondary (s1) proximally in eight species, a pattern that is very common to birds (Pyle 1997, 2008). In Blue-crowned

Lory it proceeded bilaterally from s5, as known in Psittaciformes (Pyle 2013a), and in Purple-capped Fruit-Dove, an additional proximal wave proceeded from s5, a sequence typical of species showing diastataxy or evolutionary loss of a secondary between s4 and s5 (Pyle 2008), including *Ptilonopus* doves (Bostwick and Brady 2002). Sequence among the tertials proceeded bilaterally from a node at the second tertial (t2) in all species except White-rumped Swiftlet, in which tertial sequence was not documented. Tertial molt also proceeded distally from a node at the innermost tertial (t1) in two species, occurring in 48% of 19 Collared Kingfishers and 11% of 150 Wattled Honeyeaters. A molt node primarily at t2 and secondarily at t1 has also been found in both non-passerine (Pyle 2013a) and passerine (Rohwer 2008; G. David and PP, unpubl. data) birds. It is currently unknown what proximal mechanisms account for nodal feathers among tertials or other remiges, or what adaptive mechanisms could result in the variation in the commencement node.

We documented terminal molt of secondaries among s5–s6 in six of our target species. These feathers are adjacent to the tertials in five passerine species, but in Collared Kingfisher there are two extra secondaries (s7–s8) between the tertials and s5–s6. Among our passerine species, s6 was the last feather replaced in 100% of 11 Samoan Shrikebills, 77% of 13 Cardinal Honeyeaters, 80% of 136 Wattled Honeyeaters, 79% of 43 Samoan Starlings, and 86% of seven Polynesian Starlings. This replacement sequence also coincides with what is found in North American passerines, many species showing the last feather replaced as s6 but some individuals of some species having s6 replaced before s5 and sometimes before s4 (Rohwer 2008; G. David and PP, unpubl. data). It is possible that the last feather replaced simply reflects which of the two waves, distal from the tertials or proximal from s1, reaches this section of the secondary tract first, perhaps as influenced by wing structure and molt-rate factors in species or individuals. This would indicate that molt terminus may not be mechanistically fixed or have an adaptive function within molt strategies (cf. Rohwer 2008).

Suspended and/or Arrested Molts

Suspended or arrested molts were recorded in seven of our nine species (all but Collared Kingfisher and Polynesian Startling), including 34% of 38 Purple-capped Fruit-Doves, 21% of 19 Blue-crowned Lorys, 33% of nine White-rumped Swiftlets, 7% of 28 Samoan Shrikebills, 14% of 37 Cardinal Honeyeaters, 8% of 519 Wattled Honeyeaters, and 20% of 102 Samoan Starlings. In the Purple-capped Fruit-Dove, prebasic molts appeared to be arrested, with the subsequent prebasic molt commencing where the previous molt terminated and again in typical sequence, resulting in staffelmauser or stepwise molt patterns (Pyle 2006, 2008). Other tropical doves and pigeons have been recorded undergoing staffelmauser (Radley et al. 2011, Pyle et al. 2014), a molt strategy which appears to result simply from time constraints on completing a prebasic molt during the annual cycle (Shugart and Rohwer 1996) but having the ultimate adaptation of allowing more remiges to be replaced in a single molt without incurring large, flight-impairing gaps in the wing (Tucker 1991, Pyle 2005). A greater prevelance of this strategy in tropical than in temperate Columbiformes (e.g., Pyle 1997) may relate to an increased frequency of molt suspension for breeding, as found in other American Samoan species. Interestingly, we also captured one Samoan Starling showing staffelmauser-like replacement patterns, the first report of this in a passerine of which we are aware, although we concede that this one individual could represent an anomaly.

In all seven of these species, it appeared molt could be suspended for breeding or certain phases of breeding, to be resumed where it terminated before suspension. Such suspension for breeding has been noted in other birds, most notably in diurnal raptors and parrots (Pyle 2005, 2013a). For tropical species with the potential for year-round or opportunistic breeding, mechanisms triggering breeding may occur mid-molt and result in suspension, something rarely observed in passerines breeding at more temperate latitudes. Our data from Wattled Honeyeaters suggest that molt suspension for breeding happens more frequently in females than in males, perhaps as related to the onset of sex-specific breeding hormones, or because of greater breeding constraints on females than males (cf. Freed and Cann 2013). Assessments of molt suspension have not always been explored during studies of molt-breeding overlap in tropical species (e.g., Johnson et al. 2012), and we suggest that suspensions be recorded and incorporated in analyses of molt and breeding regimes (cf. Freed and Cann 2012). It is possible that molt-breeding overlap may increase when populations are stressed, perhaps especially in females (Freed and Cann 2012, 2013), and this should be considered in future studies of this interesting dynamic within the full cycle of birds.

Arrested molts are technically defined as those which are not completed before the following prebasic molt, whereas suspended molts occur within a single molt cycle. In both staffelmauser and molt suspensions, a memory variable is involved in which the sequence commences where it previously terminated. Although nothing is currently known about how such a memory variable operates in remigial molt sequences of birds (Bridge 2011), it may involve a neurological as opposed to a hormonal mechanism (Pyle 2013a). Of interest in this regard are five Wattled Honeyeaters and two Samoan Starlings in our study that appeared to arrest molt before s5 and/or s6 were replaced. These birds then initiated the next molt with the arrested feathers along with those feathers (inner primaries and tertials) that typically commence a molt sequence. Along with the Samoan Starling exhibiting a stafflemauser-like pattern, this suggests that staffelmauser and suspension for molt in passerines may share a common ancestral mechanism involving both stable phylogenetic replacement sequences (Pyle 2013a) and a memory variable acting to bridge suspension gaps. Staffelmauser and molt suspensions have been documented in a wide variety of bird families as dependent on time constraints for molting (Pyle 2006, 2008; this study), further suggesting that these are fixed molting mechanisms. Our data support the premise that similar underlying molting strategies can be expected within landbird families throughout the world, as shaped by local environmental factors and time constraints, and that resulting age criteria such as feather shapes and molt limits also show similar global patterns.

Molt-Breeding Overlap

We assessed molt-breeding overlap in individual birds using brood patch and cloacal protuberance to indicate active reproductive state. Overlapping breeding and molting seasons at the population level have been used in previous studies to assess molt-breeding overlap, but this does not always imply simultaneous breeding and molting in individuals, especially in tropical species where both molting and breeding seasons are much more protracted than typically required for an individual bird to either breed or molt (Johnson et al. 2012). Assessment of molt-breeding overlap using active reproductive condition in live individuals is preferable to previously used methodologies (Freed and Cann 2012, Johnson et al. 2012); however, scoring of brood patches and cloacal protuberances in live birds can be inconsistent between observers, often involving the assumption of an active condition in non-breeding birds (PP, pers. obs.). This may lead to falsely high rates of reported molt-breeding overlap, at the individual level, using this method.

Despite broad overlap of breeding and molting seasons at the population level, we observed little evidence of molt-breeding overlap in our sample of Samoan landbird species. Only in Wattled Honeyeater did we encounter birds showing evidence of simultaneous breeding and molting, representing 11.4% of actively breeding birds (see Johnson et al. 2012) and 6.4% of those showing evidence of active breeding or active molting. All individuals recorded simultaneously breeding and molting were just commencing or just completing molt, and we suspect that, along with the potential for misassignment of reproductive condition scores, that there are strong physiological mechanisms resulting in the separation of molting and breeding in Wattled Honeyeater and our other study species.

The annual complete or near-complete replacement of feathers in adult birds may accompany a restoration process associated with whole-body protein synthesis and suppression of the immune system as regulated in part by thyroidal activity (Murphy 1996, Kuenzel 2003). We consider it unlikely that individuals of many species would also breed while undergoing such a process. Furthermore, molt may show seasonal predominance over breeding, as suggested by the well-defined molting season in our Wattled Honeyeaters and other species despite apparent year-round or bi-modal breeding within the population. Our results further indicate that molt can be suspended and resumed, enabling opportunistic breeding when environmental conditions shift to facilitate successful reproduction.

ACKNOWLEDGMENTS

We are indebted to the U.S. Fish and Wildlife Service for providing funding through a Wildlife Restoration Grant to the American Samoa and Department of Marine and Wildlife Resources (DWMR) in American Samoa, and to DWMR for facilitating our research. The following individuals in Samoa helped in various ways: Ray Tulafono, Ruth Matagi-Tofiga, Selaina Vaitautolu-Tuimavave, Shelly Kremer, Lainie Zarones, Ruth Utzurrum, Siaifoi Faaumu, Matthew Toilolo, Adam Miles, Ailao Tualaulelei, Mark MacDonald, Sean Eagan, James Bacon, Tavita Togia, Kiolona Atanoa, Loia Tagoni, and Panini Seafa. We are extremely grateful to the National Park of American Samoa and to the following Samoan landowners for granting us permission to establish TMAPS stations on their lands: Alo Pete Steffany, Utu Ron, Wesley Tulefano, Easter Tom Bruce, the Asi family, Fuimaono Asuemu, the Lauti family, the Gurr family, the Tula family, Sau and Usu Nua, the Saunoa family, and the Fala'a family. We thank field biologists who collected data for the TMAPS Program: Alfredo Arcilla Jr., Rudy Badia, Adrienne Doyle, Siaifoi Faaumu, Simon Fitz-William, Emily Jeffreys, Samuel Jones, Daniel Lipp, Vicki Morgan, Colleen Nell, Jessie Reese, Zachary Robinson. Ropi Seumanutafa, Josh Tigilau, and Salefu Tuvalu, and PP is indebted to the managers of the following specimen collections for assistance: Museum of Vertebrate Zoology (Carla Cicero), California Academy of Sciences (Jack Dumbacher and Maureen Flannery), Western Foundation of Vertebrate Zoology (Linnea Hall and Adam Searcy), Field Museum of Natural History (John Bates), United States Museum of Natural History (Storrs Olson and James Dean), Yale Peabody Museum (Kristof Zyskowski), Museum of Comparative Zoology (Jeremiah Trimble), and the Louisiana State University (Donna Ditmann and Steve Cardiff); a travel grant from the University of California, Davis (UCD11-02122) facilitated PP's visit to eastern North American museums for this and other specimen-based research. The manuscript was improved following critical reviews from Jared Wolfe, Gabriel David, and an anonymous reviewer. We thank Rodney Siegel, Erin Rowan, Ron Taylor, and Lauren Helton of the Institute for Bird Populations (IBP) for logistical and technical support. This is IBP Contribution Number 494.

LITERATURE CITED

AMADON, D. 1942. Birds collected during the Whitney South Sea Expedition. 50. Notes on some non-passerine genera, 2. American Museum Novitates 1176:1–21.

AMADON, D. 1943a. Birds collected during the Whitney South Sea Expedition. 52: notes on some non-passerine genera, 3. American Museum Novitates 1237:1–22.

AMADON, D. 1943b. The genera of starlings and their relationships. American Museum Novitates 1247:1–16.

BANKS, R. C. 1984. Bird specimens from American Samoa. Pacific Science 38:150–169.

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

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

DESANTE, D. F., K. M. BURTON, J. F. SARACCO, AND B. L. WALKER. 1995. Productivity indices and survival rate estimates from MAPS, a continent-wide programme of constant-effort mist-netting in North America. Journal of Applied Statistics 22:935–948.

DESANTE, D. F., K. M. BURTON, P. VELEZ, AND D. FROEHLICH. 2012. MAPS manual: 2012 protocol. Instructions for the establishment and operation of constant-effort bird-banding stations as part of the Monitoring Avian Productivity and Survivorship (MAPS) program. The Institute for Bird Populations, Point Reyes Station, California, USA.

DESANTE, D. F., T. S. SILLETT, R. B. SIEGEL, J. F. SARACCO, C. A. ROMO DE VIVAR ALVAREZ, S. MORALES, A. CEREZO, D. R. KASCHUBE, M. GROSSELET, AND B. MILÁ. 2005. MoSI (Monitoreo de Sobrevivencia Invernal): assessing habitat-specific overwintering survival of Neotropical migratory landbirds. Pages 926–936 *in* Bird conservation implementation and integration in the Americas: proceedings of the third international Partners in Flight conference. Volume 2 (C. J. Ralph and T. D. Rich, Editors). USDA, Forest Service, General Technical Report PSW-GTR-191. Pacific Northwest Research Station, Portland, Oregon, USA.

FREED, L. A. AND R. L. CANN. 2009. Negative effects of an introduced bird species on growth and survival in a native bird community. Current Biology 19: 1736–1740.

FREED, L. A. AND R. L. CANN. 2012. Changes in timing, duration, and symmetry of molt of Hawaiian forest birds. PLoS One 7:e29834. doi:10.1371/journal.pone.0029834

FREED, L. A. AND R. L. CANN. 2013. Females lead population collapse of the endangered Hawaii Creeper. PLoS One 8:e67914. doi:10.1371/journal.pone.0067914

HIGGINS, P. J. (EDITOR). 1999. Handbook of Australian, New Zealand and Antarctic birds. Volume 4: parrots to Dollarbird. Oxford University Press, Melbourne, Australia.

HIGGINS, P. J., J. M. PETER, AND S. J. COWLING (EDITORS). 2006. Handbook of Australian, New Zealand and Antarctic birds. Volume 7: Boatbill to starlings. Oxford University Press, Melbourne, Australia.

HIGGINS, P. J., J. M. PETER, AND W. K. STEELE (EDITORS). 2001. Handbook of Australian, New Zealand and Antarctic birds. Volume 5: tyrant-flycatchers to chats. Oxford University Press, Melbourne, Australia.

HOWELL, S. N. G., C. CORBEN, P. PYLE, AND D. I. ROGERS. 2003. The first basic problem: a review of molt and plumage homologies. Condor 105:635–653.

HUMPHREY, P. S. AND K. C. PARKES. 1959. An approach to the study of molts and plumages. Auk 76:1–31.

JOHNSON, E. I., P. C. STOUFFER, AND R. O. BIERREGAARD JR. 2012. The phenology of molting, breeding and their overlap in central Amazonian birds. Journal of Avian Biology 43:141–154.

JOHNSON, E. I., J. D. WOLFE, T. B. RYDER, AND P. PYLE. 2011. Modifications to a molt-based ageing system proposed by Wolfe et al. (2008). Journal of Field Ornithology 82:422–424.

JUNDA, J. H., A. L. CRARY, AND P. PYLE. 2012. Two modes of primary replacement during prebasic molt of Rufous Fantails *Rhipidura rufifrons*. Wilson Journal of Ornithology 124:680–685.

KUENZEL, W. J. 2003. Neurobiology of molt in avian species. Poultry Science 82:981–991.

MAYR, E. 1933. Birds collected during the Whitney South Sea Expedition. 24: notes on Polynesian flycatchers and a revision of the genus *Clytorhynchus* Elliot. American Museum Novitates 628:1–21.

MAYR, E. 1941. Birds collected during the Whitney South Sea Expedition. 47: notes on the genera *Halcyon*, *Turdus* and *Eurostopodus*. American Museum Novitates 1152:1–7.

MAYR, E. 1942. Birds collected during the Whitney South Sea Expedition. 48: notes on the Polynesian species of *Aplonis*. American Museum Novitates 1166:1–6.

MURPHY, M. E. 1996. Energetics and nutrition of molt. Pages 158–198 *in* Avian energetics and nutritional ecology (C. Carey, Editor). Chapman and Hall, New York, USA.

PRATT, H. D. 2010. Revisiting species and subspecies of island birds for a better assessment of biodiversity. Ornithological Monographs 67:79–89.

PYLE, P. 1997. Identification guide to North American birds. Part 1. Columbidae to Ploceidae. Slate Creek Press, Bolinas, California, USA.

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. Staffelmauser and other adaptive strategies for wing molt in larger birds. Western Birds 37: 179–185.

PYLE, P. 2008. Identification guide to North American birds. Part 2. Anatidae to Alcidae. Slate Creek Press, Point Reyes Station, California, USA.

PYLE, P. 2013a. Evolutionary implications of synapomorphic wing-molt sequences among falcons (Falconiformes) and parrots (Psittaciformes). Condor 115:593–602.

PYLE, P. 2013b. Updated manual for ageing and sexing landbirds of American Samoa. The Institute for Bird Populations, Point Reyes Station, California, USA.

PYLE, P., A. ENGILIS JR., AND D. A. KELT. 2015. Manual for ageing and sexing landbirds of Bosque Fray Jorge National Park and north-central Chile, with notes on range and breeding seasonality. Special Publication of the Museum of Natural Science, Louisiana State University, Baton Rouge, USA.

PYLE, P., A. MCANDREWS, P. VELÉZ, R. L. WILKERSON, R. B. SIEGEL, AND D. F. DESANTE. 2004. Molt patterns and age and sex determination of selected southeastern Cuban landbirds. Journal of Field Ornithology 75: 136–145.

PYLE, P., N. S. ARCILLA, K. TRANQUILLO, K. KAYANO, A. DOYLE, S. JONES, D. KASCHUBE, R. TAYLOR, AND E. ROWAN. 2014. The Tropical Monitoring Avian Productivity and Survivorship (TMAPS) program in American Samoa: 2014 report. The Institute for Bird Populations, Point Reyes Station, California, USA.

RADLEY, P., A. L. CRARY, J. BRADLEY, C. CARTER, AND P. PYLE. 2011. Molt patterns, biometrics, and age and gender classification of landbirds on Saipan, Northern Mariana Islands. Wilson Journal of Ornithology 123:588–594.

ROHWER, S. 2008. A primer on summarizing molt data for flight feathers. Condor 110:799–806.

RYDER, T. B. AND J. D. WOLFE. 2009. The current state of knowledge on molt and plumage sequences in selected Neotropical bird families: a review. Ornitología Neotropical 20:1–18.

SARACCO, J. F., J. A. ROYLE, D. F. DESANTE, AND B. GARDNER. 2012. Spatial modeling of survival and residency and application to the Monitoring Avian Productivity and Survivorship program. Journal of Ornithology 152 (Suppl. 2):S469–S476.

SHUGART, G. W. AND S. ROHWER. 1996. Serial descendant primary molt or Staffelmauser in Black-crowned Night-Herons. Condor 98:222–233.

STRESEMANN, E. AND V. STRESEMANN. 1966. Die Mauser der Vögel. Journal für Ornithologie 107(Suppl.): 1–448.

TUCKER, V. A. 1991. The effect of molting on the gliding performance of a Harris' Hawk (*Parabuteo unicinctus*). Auk 108:108–113.

WOLFE, J. D. AND P. PYLE. 2012. Progress in our understanding of molt patterns in Central American and Caribbean landbirds. Ornitología Neotropical 23:169–175.

WOLFE, J. D., P. PYLE, AND C. J. RALPH. 2009. Breeding seasons, molt patterns, and gender and age criteria for selected northeastern Costa Rican resident landbirds. Wilson Journal of Ornithology 121:556–567.

WOLFE, J. D., T. B. RYDER, AND P. PYLE. 2010. Using molt cycles to categorize the age of tropical birds: an integrative new system. Journal of Field Ornithology 81:186–194.