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MOLTS AND PLUMAGES IN THE LONG-TAILED AND OTHER JAEGERS: AN “ALTERNATE” EXPLANATION FOR NONBREEDING PLUMAGES?

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ABSTRACT: Jaegers molt at sea, and these poorly known molts result in variable and confusing fall and winter plumages. We summarize the progression of molts and appearance of the plumages in 11 Long-tailed Jaegers (*Stercorarius longicaudus*), of four age groups, photographed off Chile in December 1993. The central rectrices in these birds were short, blunt-tipped, and either plain brown or boldly barred black and white, indicating that, in at least some individuals, these feathers were replaced for a second time within the molt cycle. The body plumage of five adults was quite different from the breeding plumage and differed from nonbreeding plumages depicted in the literature. Individuals replacing primaries during the second prebasic molt showed worn and bleached head and body feathers, indicating only limited feather replacement since the preformative molt rather than a complete body molt in their second fall as widely reported. Examination of 647 specimens confirmed that in jaegers body-feather molt is partial to incomplete in fall and usually complete in spring. Using the Humphrey–Parkes nomenclature, we thus propose a novel molt and plumage terminology for jaegers, in which birds breed in basic plumage and undergo a partial prealternate body molt in fall. Under this interpretation, a limited first prealternate body-feather molt occurs during the second summer and fall, and the first cycle is completed at an age of 15–18 months. The later and complete preformative molt, from November to March, produces stronger formative feathers, allowing the second prebasic body molt to be “pushed back” by 6 months, leading to a spring-to-spring cycle of prebasic molt. We suggest that a prealternate body-feather molt has evolved in jaegers to provide protective coloration for flight-feather molt, as has been proposed for ducks and ptarmigan, or perhaps for social signaling or just to replace feathers that wear quickly because of intense annual solar exposure.



Figure 1. Long-tailed Jaegers, 5 km off Arica, Chile, 2 December 1993, showing variation in nonbreeding plumages of one first-cycle, three second-cycle, one probable third-cycle, and one definitive-cycle birds (from left to right, birds 2C3, 3C1, 2C1, 1C1, 2C2, and DC3 in Table 1). Note the bleached whitish heads of the second-cycle birds.

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Figure 2. Second-cycle Long-tailed Jaeger, 5 km off Arica, Chile, 2 December 1993 (bird 2C4 in Table 1). Note the bleached head feathers, incomplete back molt, worn pointed central rectrix, and suspension limit between p7 and p8 of the formative plumage.

Photo by Martin Reid

Adult Long-tailed Jaegers (*Stercorarius longicaudus*) migrate to their arctic and subarctic breeding grounds in fresh “breeding” plumage and return to their Southern Hemisphere winter range in the same plumage. As a result, the species’ “nonbreeding” plumages are typically worn only at sea in the Southern Hemisphere and are under-represented in specimen collections. Descriptions and illustrations of the Long-tailed Jaeger’s adult nonbreeding plumage are variable and conflicting; most indicate it to resemble the adult breeding plumage, including a blackish cap and pale yellowish to whitish hind collar, but to be muted in color and/or to show indistinct barring to the sides, flanks, and undertail coverts (e.g., Cramp 1983, Higgins and Davies 1996, Malling Olsen and Larsson 1997, Dunn and Alderfer 2011, Sibley



Figure 3. Long-tailed Jaegers, 5 km off Arica, Chile, 2 December 1993 (from left to right, birds DC3, 2C3, DC4, and 1C1 in Table 1). Note the bleached head feathers and underwing pattern of the second-cycle bird (2C3) and the incomplete back molt in the right-hand definitive-cycle bird (DC4).

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2014). Wiley and Lee (1998), Howell (2007), and Pyle (2008) described it as resembling nonbreeding plumages of the second and/or third-cycles but provided little detail. This adult “nonbreeding” plumage has universally been considered the definitive (or adult) “basic plumage” by those using the molt and plumage terminology of Humphrey and Parkes (1959; “H-P”) (Higgins and Davies 1996, Wiley and Lee 1998, Howell, 2007, 2010, Pyle 2008).

The Long-tailed Jaeger molts at sea, primarily in the Southern Hemisphere, and accounts of the timing and extents of these molts are variable and confusing. In adults, generally, a molt of body feathers takes place from September to December, followed by a protracted molt of flight feathers from November to March, and then a molt of body feathers from March to May (Cramp 1983, Higgins and Davies 1996, Malling Olsen and Larsson 1997, Wiley and Lee 1998, Howell 1999, 2007, Pyle 2008). The “fall” (throughout our use of seasons refers to those of the Northern Hemisphere) body-feather molt may overlap the beginning of primary molt, and the “spring” body-feather molt may overlap the end of primary molt (Melville 1985, Howell 2007). There is little specific information on the extent of these two body-feather molts in any species of jaeger, and there is confusion about whether or not the ornamental central rectrices are replaced once or twice within a definitive molt cycle (Cramp 1983, Howell 2007, Pyle 2008); breeding-plumaged jaegers appear to show only one generation of rectrices (Pyle pers. obs. during specimen examination). The most detailed information on the Long-tailed Jaeger’s winter molts and plumages is based on 16 beach-cast birds in New Zealand, found primarily in 1983 during El Niño (Melville 1985), at which time they may not have been molting normally (cf. Howell and Corben 2000).

Table 1 Summary of Long-tailed Jaegers Photographed off Chile on 2 December 1993

Bird	Primaries ^a	Rectrices ^b	Head plumage	Bill base	No. of Images
1C1	p1; rest juvenile	r1 brown (F)	dark	pale	5
2C1	p2; even cline	r1 brown (F)	white; pale gray cap	pale	2
2C2	p3; even cline	r1 brown (F)	white; pale gray cap	slightly pale	5
2C3	p4; even cline	r1 brown (F?)	white; pale gray cap	unknown	4
2C4	p5; susp. p7-8	r1 brown (F)	white; pale gray cap	slightly pale	4
3C1	p6; even cline	r1-r2 barred (A2)	dark; white nape	slightly pale	2
DC1	p2; even cline	r1 barred (DA)	streaked dusky; pale nape	dark	1
DC2	p3; susp. p6-7	r1-r2 barred (DA)	pale grayish; darker cap	dark	2
DC3	p4; even cline	r1 brown (DA)	plain gray	dark	9
DC4	p5; even cline	r1 brown (DA)	grayish; darker cap	dark	6
DC5	p6; even cline	r1 brown (DA)	grayish; darker cap	dark	10

^aPrimaries (p) numbered from inner (p1) to outer (p10). Primary specified is the outermost dropped during molt, followed by appearance of the unmolted outer primaries, whether juvenile, worn in a smooth progression (even cline) from inner out, or worn unevenly, implying a suspension (“susp”) of the previous molt between the adjacent primaries specified.

^bRectrices numbered from the central pair (r1) out. The presumed generation of r1 is categorized as juvenile (J), formative (F), second alternate (A2), or definitive alternate (DA), under the alternative interpretation of molt cycles we present (see Figure 5).

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On 2 December 1993, Reid obtained 23 photographs of Long-tailed Jaegers from a flock of 11 birds encountered about 5 km west-southwest of Arica, northern Chile. They were the only Long-tailed Jaegers he observed during 4.25 hours of observation while traveling 30 km and out to about 10 km off shore. The birds' head and body plumage was unlike that shown in field guides (e.g., Dunn and Blom 1983) for adults (Figure 1), leading Reid to assume that these jaegers were in their first or second cycle. However, examination of the underwing coverts and contrasts in the primaries representing cycles of molt (cf. Pyle 2008) indicated that the flock consisted of only one first-cycle bird (age 6 months), four second-cycle birds (age 1.5 years), one probable third-cycle bird (age 2.5 years), and five definitive-cycle adults (photos on this issue's inside and outside back cover; Figures 1–4). All of the birds were undergoing replacement of primaries. Here we discuss the molt strategies and variation in the nonbreeding plumages of the Long-tailed and other jaegers, as documented by these photographs and examination of specimens. In the process, we propose a novel interpretation of molt and plumage terminology in jaegers, suggesting that the alternate plumage is worn in winter and breeding birds are in basic plumage.

ANALYSIS OF IMAGES

Among the 23 photos are 50 depictions of the 11 Long-tailed Jaegers. Careful comparison of plumage, molt progression, and positioning of the birds with respect to the sequence of photographs allowed us to identify each individual with confidence. We designated each individual, by cycle, as 1C1 (first-cycle bird); 2C1, 2C2, 2C3, and 2C4 (second-cycle birds); 3C1 (prob-



Figure 4. Presumed third-cycle Long-tailed Jaeger, 5 km off Arica, Chile, 2 December 1993 (bird 3C1 in Table 1). Note that the head plumage is darker and barring on the underwing is less extensive than in the second-cycle birds in Figures 1–3. Note also the relatively advanced primary molt (to p6) and the two pairs of barred central rectrices.

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able third-cycle bird); and DC1, DC2, DC3, DC4, and DC5 (definitive-cycle adults). The number of photos in which an individual was identified varied from one (DC1) to 10 (DC5) of the 23 total. We summarize the number of images, molt status, and appearance of each of these 11 birds in Table 1.

As expected, molt proceeded from the innermost (p1) toward the outermost (p10) primary in all 11 birds. The most distal growing or dropped primary, marking the progression of molt, ranged from p1 (in 1C1) to p6 (in 3C1 and DC5). In the second-cycle birds it ranged from p2 to p5, in the adults from p2 to p6 (Table 1; Figure 2; photos on this issue's outside and inside back covers). Of the 10 birds in their second cycle or older, eight showed an even progression toward fresher unmolted primaries to the outside, indicating uninterrupted replacement of those primaries during the previous molt (Figure 3; this issue's back cover). The remaining two individuals, 2C4 (Figure 2) and DC2, showed "suspension limits" (cf. Pyle 2005a, 2008) between p6 and p9, contrasts between a worn primary and a much fresher adjacent distal feather. These limits indicate that molt of primaries had begun, was suspended for an extended period, and then resumed later within the cycle.

The central rectrices showed two distinct color patterns (Table 1). Three birds in their third or later cycle (3C1, DC1, and DC2) had boldly barred dark-and-white central rectrices (Figure 4; bottom photo on this issue's outside back cover). These feathers were short, extending <100 mm beyond the other rectrices, and were pointed but not as attenuated at the tips as in the ornamental central rectrices of the breeding plumage. Two of these three individuals, 3C1 (Figure 4) and DC2, showed two pairs of barred central rectrices (r1 and r2), whereas DC1 (outside back cover, bottom photograph) showed just the innermost pair (r1) barred, with r2 of the same generation as r3-r6.

In the remaining seven individuals the central rectrices were brown, as in the breeding plumage. In the first-cycle bird (1C1) the central rectrices appeared to be growing and had tips less attenuated than in breeding adults, and on the second-cycle birds (2C1-2C4; e.g., Figure 2) they were worn, extended about 100 mm beyond the other rectrices, and had tips similar to those of the first-cycle bird. We infer that these were growing and worn feathers of the formative plumage, respectively. On the remaining three birds with unbarred rectrices, DC3, DC4, and DC5 (e.g., upper image on inside back cover), the central rectrices were newer than adjacent rectrices, extended 100-200 mm beyond these other rectrices, and were blunter at the tip than found in breeding adults.

The head plumage was dark in the first-cycle bird (Figures 1, 3), bleached whitish with a grayish mottled crown in the four second-cycle birds (Figures 1-3; upper photos on inside and outside back cover), and dark with a pale nape on the third-cycle bird (Figure 4). In the definitive-cycle adults the head varied from somewhat plain gray to streaked dusky with a pale nape (Table 1; Figures 1, 3; inside and outside back cover). The photographs indicate that the previous head-feather molt in the second-cycle birds was absent to limited and back-feather molt in these and the older birds was limited to incomplete, the backs showing a mixture of both newer and much older feathers (Figures 2 and 3; inside back cover, upper photo). The base of the bill was distinctly paler than the tip on the first-cycle bird, slightly paler than the tip on the second-cycle and third-cycle birds, and uniformly black on

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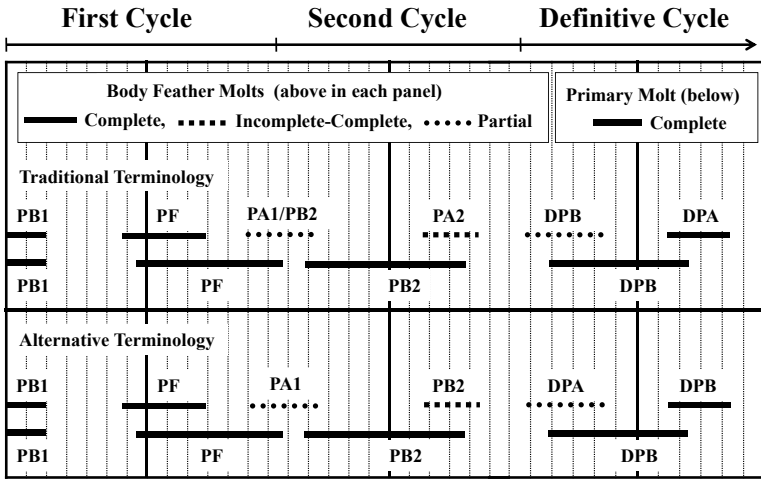


Figure 5. Molt strategies of the jaegers during the first, second, and definitive cycles, as expressed in traditional terminology and the alternative we propose. PB1, first prebasic molt; PF, preformative molt; PA1, first prealternate molt; PB2, second prebasic molt; DPB, definitive prebasic molt; DPA, definitive prealternate molt.

the definitive-cycle adults (Table 1). All the birds had legs of a similar color pattern, pale bluish with black feet and black on and above the above the intertarsal joint (Figure 3; inside and outside back cover).

The third-cycle bird (Figure 4) appeared to have mostly dark underwing coverts but with some slightly barred feathers among the lesser coverts, matching the third-cycle underwing coverts as described by Howell (2007) and Pyle (2008). As this bird's primary molt had progressed to p6, it could also have been a second-cycle bird that had already replaced many underwing coverts and had developed head plumage more advanced (darker) than the other second-cycle individuals. Provided that third-cycle birds can be consistently and reliably aged (see Pyle 2008), however, this bird seems more likely to have been in its third winter because of its replaced central rectrices, which are not otherwise found in second-cycle Long-tailed Jaegers (Table 1 and see below). The second-cycle birds showed boldly barred (formative) underwing coverts; at least three of these, 2C1, 2C2, and 2C4, appeared also to show newer, more boldly barred, axillars contrasting with older underwing coverts (Figures 2, 3; upper photos on outside and inside back cover). The first-cycle bird had finely barred underwing coverts (Figure 3) and the adults had uniformly dark underwing coverts, as described by Howell (2007) and Pyle (2008).

VARIATION IN LONG-TAILED JAEGER MOLTS AND PLUMAGES

The progress of flight-feather molt, as inferred from these photographs, generally accords with that of the literature on the Long-tailed Jaeger; how-

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Figure 6. Specimens of jaegers collected during their second fall and winter. Top, Long-tailed Jaeger (CAS 16402) collected in Monterey Bay, California, 4 October 1909; center, Parasitic Jaeger (MVZ 17834) collected in Monterey Bay, 12 December 1910; bottom, Long-tailed Jaeger (SDNHM 41733) collected 69 km east of Cocos Island off Costa Rica, 26 January 1980. These birds are entirely (top) or primarily in worn formative plumage at ages of 16–19 months with limited replacement of back feathers in second fall in the center and bottom specimens.

Photos by Peter Pyle (top and center) and Philip Unitt (bottom)

ever, its timing varies substantially in both the second and definitive cycles. Molt of the primaries can commence as early as late November in the first cycle (later than generally reported), and from August to November in later cycles, as reported (Cramp 1983, Higgins and Davies 1996, Malling Olsen and Larsson 1997, Wiley and Lee 1998, Howell 2007, Pyle 2008). We saw little indication that the second-cycle birds had commenced primary molt before the adults, as has been reported; however, the third-cycle bird had progressed to p6, indicating a start to the molt earlier than that of most adults.

Two birds, whose molt had progressed to p2 and p5, also showed suspension limits between p6 and p9 of the previous generation. We suggest that these birds had suspended molt of primaries for the northbound migration of the previous spring, then resumed it on their summer grounds in the Northern Hemisphere. Melville (1985) suggested suspension of molt in one New Zealand specimen but otherwise we have not found previous mention of it in jaegers or skuas.

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Figure 7. Specimens of second-summer (two years old; left two birds) and adult Long-tailed Jaegers (right) collected in Alaska during the breeding season. Left, MVZ 136444, collected at Barrow, 17 June 1957; center, MVZ 136452, collected near Barrow, 18 July 1957; right, MVZ 31474, collected at the Kowak River delta, 17 June 1899. The second spring body-feather molt is often incomplete, with retained feathers being either barred white or plain brown; the former appear to represent feathers replaced earlier, the latter feathers replaced later during the first fall molt. Over 96% of adult jaegers examined had undergone a complete spring molt, as in the right-hand bird.

Photo by Peter Pyle

Reid's photos also confirm that the central pair or two of rectrices can be replaced twice during the third and later cycles. In the Long-tailed Jaeger's nonbreeding plumages the central rectrices are relatively broad tipped and short, and can either be brown or barred black and white, the latter pattern substantially different from that of the breeding plumage. Melville (1985) noted that about half of the Long-tailed Jaegers that washed up in New Zealand in January and February 1983 had barred central rectrices; this is the only other reference we can find for this pattern.

The nonbreeding plumage of the head appeared to vary by age. The head was dark with a pale nape in the first-cycle bird but bleached and whitish in the four second-cycle birds, a difference not previously reported. The third-cycle bird and adults, in turn, showed variable head plumage, rather plain gray to streaked dusky, unlike the nonbreeding plumage depicted in most field guides (e.g., Dunn and Alderfer 2011, Sibley 2014). These photos

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also suggest that the bill color may vary with age more than does leg color, *contra* Pyle (2008). During molt of the primaries, the leg color may be a less reliable clue to the bird's age, the color of adults' legs reverting to resemble that of first-cycle birds, as has been found in herons, gallinules, and some other waterbirds (Pyle 2008).

AN "ALTERNATE" TERMINOLOGY FOR NONBREEDING JAEGERS?

The prebasic molt, as defined by Humphrey and Parkes (1959), typically includes all body feathers and most or all flight feathers (Pyle 1997, 2008, Howell 2010). It appears to be part of an ancestral process of physical restoration including epidermal, bone, and muscle tissues, evolved from a similar process (ecdysis) in reptiles (Murphy 1996, Pyle 2013b). Analysis of the photos from Chile suggests that the fall body and rectrix molt, which precedes molt of the remiges, is not complete in jaegers. Ducks and ptarmigan also have two body-feather molts overlapping the flight-feather molt, and in both groups the first body-feather molt is variably limited to partial whereas the second body-feather molt is complete and should be included with the flight-feather molt as part of the prebasic molt (Pyle 2005b, 2007). If the body-feather and remex molts of the jaegers are similar to those of ducks, jaegers may also be considered to breed in basic plumage, a novel interpretation of molt terminology for the Stercorariidae. To investigate this possibility further, Pyle examined 647 specimens of the Long-tailed, Parasitic (*S. parasiticus*), and Pomarine (*S. pomarinus*) jaegers at the California Academy of Sciences (CAS), Museum of Vertebrate Zoology (MVZ), and Western Foundation of Vertebrate Zoology (WVZ), along with photographs of a key specimen at the San Diego Natural History Museum (SDNHM).

Molt Strategies in the Jaegers

Molt in the jaegers during the first, second, and definitive cycles, based on photographs and specimen evidence, is summarized in Figure 5. All three species follow an apparently similar strategy. On average, molt of the primaries and body feathers begins earlier in the Pomarine than in the Parasitic Jaeger, which in turn begins earlier than in the Long-tailed Jaeger. These differences are likely related to the average latitude at which the species winters, as in shorebirds (Pyle 2008:500–505), as well as a need for the larger species to commence molt earlier in order to complete flight-feather growth within the time constraints of the season available. Otherwise, the differences in timing and extents of body-feather molts relative to primary molts appear to be similar (as shown in Figure 5), so we discuss the three species jointly.

Following the complete prejuvenile (first prebasic) molt at the nest, first-cycle jaegers undergo a complete preformative molt of body feathers from November to March and of wing feathers from December to May or later. Of 42 juvenile jaegers collected between 21 August and 4 November, none had begun body-feather molt. In 22 worn first-cycle specimens collected before the next year's fall molt had begun (11 Parasitic Jaegers, 10 Pomarine Jaegers, and one Long-tailed Jaeger), from 16 April to 4 October, formative body-feather molt was complete. Variability in individual feathers' degree of wear implies that this molt is protracted. Formative back feathers

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with more wear (replaced earlier) were dark with pale fringing (similar to juvenile feathers) whereas fresher feathers (replaced later) appeared more uniformly brown.

Careful examination of photographs and specimens taken during the bird's second summer, fall, and winter (age 12–18 months) indicate that formative-plumaged jaegers only undergo a single limited to partial body-feather molt in summer and fall (Figure 6), rather than a limited spring and complete fall body-feather molt reported in the literature (Cramp 1983, Higgins and Davies 1996, Malling Olsen and Larsson 1997, Wiley and Lee 1998, Howell 2007, Pyle 2008). This molt can commence as early as the first week of June (Pomarine Jaeger CAS 10957, Parasitic Jaeger WFVZ 50394) but more typically in July, as all of 17 specimens collected in August (8 Parasitic and 9 Pomarine jaegers) had begun the molt. On the basis of 69 specimens (38 Parasitic and 31 Pomarine jaegers), collected off California between 12 August and 25 October, this body-feather molt appears to terminate by early to mid September. It often commences, and in some cases may end, before all juvenile primaries have been replaced (as late as 7 October; Pomarine Jaeger CAS 10951 with p9 growing and p10 juvenile). The head plumage consists of uniformly worn formative feathers in all but one of these specimens (Pomarine Jaeger CAS 11006, collected 22 August with a few crown feathers replaced), whereas the feathers of the upper back, sides, and flanks were variably and partially replaced. The central rectrices were formative in all 31 of these Parasitic Jaegers but at least one of the two feathers had been replaced with a blunt-tipped second-fall rectrix in 13 of the 38 Pomarine Jaegers. The only specimen of the Long-tailed Jaeger collected during the second fall was in worn formative plumage and had not begun a second-fall body-feather molt by 4 October (Figure 6, top). None of the four second-cycle birds photographed off Chile on 2 December had replaced central rectrices during this molt (Table 1).

Photographs and specimens of jaegers taken during their second winter are few, but all show bleached formative head feathers and a variable mixture of newer barred feathers and older formative feathers in the upperparts, sides, and flanks, further indicating that only a few feathers were replaced during the second-fall molt (Figures 1–3 and 6; back cover). A Parasitic Jaeger photographed in November (Malling Olsen and Larsson 1997:132, figure 82) similarly appears to be in bleached formative plumage with a few upperpart feathers replaced. Thus jaegers retain most of the formative body plumage when the second prebasic molt of the primaries commences, primarily from August to November. Second-fall back feathers replaced earlier (e.g., June and early July) are dark with bold white bars or markings, whereas feathers replaced later (e.g., late August and September) may be unmarked (Figures 2, 6; Malling Olsen and Larsson 1997: figure 82).

The second prebasic molt of the remiges takes place primarily from September to March, although it may begin as early as 24–26 July (Parasitic Jaeger MVZ 140053, Pomarine Jaeger MVZ 54193) and as late as February in the Long-tailed Jaeger—SDNHM 41733, collected 26 January, had not yet begun molt of primaries (Figure 6, bottom). A body-feather molt then takes place in the bird's second spring, probably from February to May, and can be incomplete or complete in all three species (e.g., Figure 7). Among

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Figure 8. Specimens of winter adult Pomarine Jaegers collected in Monterey Bay, California, showing incomplete definitive fall body-feather molt. Left, CAS 11031, collected 8 November 1907; center, CAS 16399, collected 9 December 1909; right, CAS 16134, collected 13 December 1909. From left to right, the progression of molt of the primaries was to p5, p6, and p7, and the proportion of back feathers replaced in the fall body-feather molt was an estimated 40%, 50%, and 80%, respectively.

Photo by Peter Pyle

two-year-olds collected off California from May to September, 3 of 9 Long-tailed Jaegers, 27 of 30 Parasitic Jaegers, and 14 of 18 Pomarine Jaegers had undergone an incomplete second-spring body-feather molt (Figure 7), while the remainder had undergone a complete molt. The retained feathers on the birds with incomplete second-spring molts were either barred and worn or unbarred and fresher (Figure 7), having been replaced earlier or later in the bird's second fall, respectively.

The third-fall body-feather molt can begin as early as 25 June (Parasitic Jaeger CAS 11080). In adults the fall body-feather molt can begin as early as 2 July (Pomarine Jaeger MVZ 140051) or as late as early October (Parasitic Jaeger CAS 15943, collected 2 October, had not begun this molt). About half of specimens collected in August and 75% of those collected in September had begun the fall body-feather molt. On the basis of feather wear, this molt appears to be completed by November (Figure 8). Among the few winter adults examined that were undergoing definitive prebasic molt of the primaries, body-feather molt had been variable, with the proportion of feath-

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ers replaced ranging from about 40% of upper back and half of the flank feathers to nearly complete but with at least some larger scapulars and flank feathers retained from the summer plumage (Figures 3 and 8; upper image on the inside back cover; six Parasitic Jaegers collected off Chile in January and February at WFVZ). Melville (1985) also reported that adult Long-tailed Jaegers collected in January had mixed generations of upperpart feathers.

As in previous cycles, definitive prebasic molt of primaries occurs largely from August to March and averages earlier in the Pomarine Jaeger, later in the Long-tailed Jaeger. Adults' spring body-feather molt begins as early as late February (WFVZ 48544, collected 28 February) and extends into early April, earlier than generally reported (e.g., Pyle 2008). This body-feather molt is complete in virtually all birds (Figure 7). Among specimens collected from May to September, 65 of 67 Long-tailed Jaegers, 77 of 79 Parasitic Jaegers, and 106 of 112 Pomarine Jaegers (96.1% overall) had undergone a complete definitive spring body-feather molt. The remainder of these specimens retained one to a few body feathers that had been replaced the previous fall. A few adults (both with and without body feathers retained), primarily Pomarine Jaegers, had also retained up to a few greater coverts or secondaries.

Whether the back feathers and central rectrices replaced during a jaeger's second fall are barred (as in a juvenile) or uniformly brown (as in an adult) appears to be controlled by a hormonal switch, perhaps sometime between August and October. Such "molt-plumage interactions" were discussed for the Common Murre (*Uria aalge*) by Pyle (2013a) and mentioned for jaegers by Howell (2007) and Pyle (2008). Hormonal switches affecting feather patterns and shape over the course of protracted molts appears to explain the variability in jaegers' nonbreeding plumages.

An Alternative Molt Terminology

The timing of primary molts and the extent of the preformative molt based on specimens we examined (Figure 5) largely accords with that reported in the literature (Cramp 1983, Higgins and Davies 1996, Malling Olsen and Larsson 1997, Wiley and Lee 1998, 1999, 2000, Howell 2007, Pyle 2008). However, we found that the number of body feathers and central rectrices replaced during fall molts is variable, whereas spring body-feather molt in many third-cycle birds and virtually all adults is complete (Figure 5). This contrasts with information in the literature cited above, which indicates the fall body molt to be complete and the spring molt to be partial and which aligns the fall body-feather molt with the wing molt to form the complete (prebasic or post-breeding) molt. Under this interpretation, however, either one or two pairs of central rectrices (r1 and r2) and some axillars may or may not have been replaced in fall, followed by a complete rectrix and underwing-feather molt in spring, resulting in an indeterminable number of alternate feathers among these uniformly replaced tracts in breeding birds. This explains previous confusion by Cramp (1983), Pyle (2008), and others over how many times a jaeger's central rectrices are replaced per molt cycle.

Solely on the basis of completeness, as directed by Humphrey and Parkes (1959), the complete or nearly complete spring body-feather molt of jaegers

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thus should be considered part of a definitive prebasic molt, and the partial-to-incomplete fall body-feather molt should be considered a prealternate molt, opposite that reported but paralleling similar molt sequences in ducks and ptarmigan (Pyle 2005b, 2007). Under this alternative interpretation (Figure 5), jaegers' first cycle would be extended to an age of about 18 months, longer than reported for other birds, and would include a limited first prealternate molt at 12–16 months of age followed by the more complete second prebasic body-feather molt, from February to April, concurrent with completion of the second prebasic flight-feather molt. Although, according to this interpretation, in most cases the second prebasic molt would involve complete replacement of flight feathers but incomplete replacement of body feathers, a strategy unusual for a prebasic molt, this would also be the case under traditional terminology (see Figure 5).

During the jaegers' evolution, a formerly complete fall prebasic body-feather molt may have become incomplete, and a formerly partial spring prealternate body-feather molt may have become complete, which would adhere to traditional molt terminology although we know of no other examples of this yet documented in other birds. Such a strategy would not be predicted if the prebasic molt accompanies a process of whole-body restoration including the epidermis (Pyle 2013b). Skuas, formerly of the monophyletic genus *Catharacta* but now placed with jaegers in *Stercorarius*, appear either to lack or to have a very limited prealternate or “pre-breeding” molt (Cramp 1983, Higgins and Davies 1996, Malling Olsen and Larsson 1997), which could alternatively represent the final stages of a single protracted body-feather molt (Pyle 2008, Howell 2010, Newell et al. 2013). The timing of the body-feather molt(s) is reported to coincide largely with that of replacement of the primaries, commencing earlier in some Great Skuas (*S. skua*), while beginning later than replacement of the primaries in the South Polar Skua (*S. maccormicki*; Cramp 1983, Higgins and Davies 1996, Malling Olsen and Larsson 1997, Howell 2004). Because of the dearth of specimens collected at sea, it is unclear whether skuas also molt their body feathers only partially in fall but more completely in spring, as we document here for the jaegers. At this time, therefore, we cannot infer which of the body-feather molts in jaegers is homologous with the prebasic molt in skuas, which, if skuas are ancestral to jaegers (Chu et al. 2009), could in turn reflect molt strategy in a common ancestor that lacked a prealternate molt. Switching hemispheres for breeding may have influenced or confused the evolution of molts in skuas and jaegers. However, molts appear to adapt quickly to light regimes of the opposite hemisphere, e.g., within a year in vagrants residing in the wrong hemisphere (Pyle pers. obs.). Therefore we consider it unlikely that colonizing a new hemisphere affected the long-term evolution of molt strategies substantially.

We consider it more likely that in the jaegers a prealternate body-feather molt evolved during fall, perhaps resulting in protective coloration for flight-feather molting, as has been proposed for ducks and ptarmigan (Pyle 2005b, 2007), or perhaps for social signaling or just to replace feathers that wear quickly because of exposure to intense sunlight through the year (see below). In any case, neither the timing of these molts relative to breeding nor the ensuing feather-color pattern is sufficient reason to presume that

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the fall molt is homologous with the prebasic molt, under an evolutionary interpretation of molts as proposed by the H-P system (Howell et al. 2003, 2004, Pyle 2005b, 2007, 2008, 2013b, Howell 2010).

Other birds with a prealternate molt and in which flight-feather molt is protracted over the winter include the loons, some shorebirds such as the American Golden-Plover (*Pluvialis dominica*), some gulls such as Sabine's Gull (*Xema sabini*), the puffins, the Ruby-throated Hummingbird (*Archilochus colubris*), some Eurasian shrikes, and the Red-eyed Vireo (*Vireo olivaceus*) (Howell and Pyle 2005, Pyle 1997, 2008, 2009, 2013c, Pyle et al. 2015). All of these species are subject to substantial solar exposure year round, which appears to relate to the evolution of prealternate molts in migratory species (Pyle 2008, Howell 2010). However, most of these species appear to differ from the jaegers in having partial preformative molts and/or having complete fall and partial spring definitive body-feather molts. Furthermore, congeneric or other closely related species of each of these taxa appear to have homologous molts resulting in basic plumages for the nonbreeding season. More study of molt in these species, however, might suggest H-P terminologies alternative to those currently recognized (cf. Pyle 2013c).

With respect to molts in these species, we propose that the jaegers' later and complete preformative molt, from November to March, allows an extended first cycle that results in the alternative molt strategy and nomenclature proposed in Figure 5. Most of the taxa mentioned in the previous paragraph have less complete preformative molts that occur earlier in the summer or fall, producing formative feathers in need of replacement earlier than do those of jaegers. In the loons and puffins, it appears that the second and third prebasic molts have been "pulled forward" to allow a quick transition from the third prebasic molt in summer and fall to the definitive prebasic molt in winter and spring (Howell and Pyle 2005). In the jaegers, by contrast, the second prebasic body-feather molt appears to have been "pushed back," a strategy made possible by the late and complete preformative molt, growing formative feathers stronger than those of other birds, and allowing a subsequent transition to a spring-to-spring cycle of prebasic molt.

In conclusion, examination of a series of photographs taken over 20 years ago has shed additional light on the molts, plumages, and age criteria of Long-tailed Jaegers in nonbreeding (winter) plumages, leading us to reinterpret the terminology of jaeger molt, considering the birds to breed in basic plumage and wear an alternate plumage in fall and winter. Further evidence and analysis based on winter-collected specimens is needed to solidify this reinterpretation.

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Long-tailed Jaegers (*Stercorarius longicaudus*) 5 km off Arica, Chile, 2 December 1993. Upper photo, two adults in nonbreeding plumage (left and right) and a second-cycle bird (center); note the head patterns and underwing patterns characteristic of these ages. These are birds DC3, 2C2, and DC5 in Table 1, p. 244. Lower, three adults; note the range of variation. These are birds DC3, DC5, and DC4 in Table 1, p. 244.

Photos by Martin Reid



"Featured Photos" by Martin Reid of San Antonio, Texas: Long-tailed Jaegers (*Stercorarius longicaudus*) 5 km off Arica, Chile, 2 December 1993, showing variation in the plumage of nonbreeding adults and of a bird in its second winter (upper photo, top image). Note the barred central rectrix in the lower photo. In this issue of *Western Birds*, Peter Pyle and Martin Reid unravel the complex and hitherto inadequately understood cycles of molt in the jaegers.