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RESEARCH ARTICLE

Timing and duration of primary molt in Northern Hemisphere skuas and jaegers

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ABSTRACT
We compared the primary molt of the 4 species of skuas and jaegers (Stercorariidae) that breed in the Northern Hemisphere: Long-tailed Jaeger (*Stercorarius longicaudus*), Parasitic Jaeger (*S. parasiticus*), Pomarine Jaeger (*S. pomarinus*), and Great Skua (*S. skua*). We analyzed primary molt data of 1,573 individuals of multiple age classes, mostly collected from photographs taken at sea but also from museum specimens and beached individuals. Whereas molt duration generally increased with species' size, molt duration in Parasitic and Pomarine jaegers was surprisingly similar given their size difference. Larger species started primary molt earlier and showed more overlap with postbreeding migration, such that there was complete overlap in Great Skua but no overlap in Long-tailed Jaeger. Within jaeger species, the first primary molt cycle took longer than later molt cycles. We suggest that, unlike birds in their first primary molt cycle, birds in their second or subsequent primary molt cycles are time-constrained to complete primary molt before the onset of prebreeding long-distance migration. By contrast, molt duration did not differ between age classes of Great Skuas. Adult Great Skuas may have overcome the time constraint by completely overlapping molt and postbreeding migration. Molt-migration overlap is generally rare in birds but may be feasible for Great Skuas given their shorter migration distance and low migration speed.

Keywords: annual cycles, molt-migration overlap, primary molt, Stercorariidae

Tiempo y duración de la muda primaria en especies de Stercorariidae del Hemisferio Norte

RESUMEN
Comparamos la muda primaria en cuatro especies de Stercorariidae que crían en el Hemisferio Norte: *Stercorarius longicaudus*, *S. parasiticus* y *S. pomarinus*, y *Skua skua*. Analizamos datos de la muda primaria de 1573 individuos de múltiples clases de edad, colectados mayormente a partir de fotografías tomadas en el mar pero también de especímenes de museo e individuos varados. Mientras que la duración de la muda generalmente aumentó con el tamaño de la especie, la duración de la muda de *S. parasiticus* y *S. pomarinus* fue sorprendentemente similar dadas sus diferencias de tamaño. Se encontró que las especies más grandes comenzaron la muda primaria más temprano y mostraron más superposición con la migración posterior a la reproducción, de tal manera que hubo una superposición completa en *Skua skua* pero no hubo superposición en *S. longicaudus*. Dentro de las especies de *Stercorarius*, el primer ciclo de muda primaria tomó más tiempo que los ciclos de muda posteriores. Sugerimos que, a diferencia de las aves en su primer ciclo de muda primaria, las aves en su segundo ciclo o en ciclos subsecuentes de muda primaria están limitadas por el tiempo para completar la muda primaria antes del inicio de la migración de larga distancia previa a la reproducción. En contraste, la duración de la muda no difirió entre las clases de edad en *S. skua*. Los adultos de *S. skua* pueden haber superado la restricción de tiempo superponiendo completamente la muda y la migración posterior a la reproducción. La superposición entre muda y migración es por lo general rara en las aves pero puede darse en *S. skua* debido a su corta distancia y a su baja velocidad de migración.

Palabras clave: ciclos anuales, muda primaria, Stercorariidae, superposición entre muda y migración

INTRODUCTION

Primary molt, the replacement of the large remiges attached to the "hand" of the wing, is one of the major events in the annual cycle of all birds. Several strategies have evolved to fit molt into a bird's annual cycle, generally avoiding temporal overlap with other demanding activities such as breeding and migration (Hedenström 2006). Non-

overlap may be achieved by adjusting the timing of molt (e.g., postponing molt until after the most intense period of chick care, or after migration) or by shortening the duration of molt (usually by growing more feathers simultaneously; Rohwer and Rohwer 2013). Speeding up of molt can lead to decreased flight performance (Hedenström and Sunada 1999) or a lower quality of feathers (Dawson et al. 2000, Serra 2001).

Most variation in molt duration between species is explained by body size (larger species taking longer to molt; Rohwer et al. 2009), whereas molt duration and timing may vary between and within species according to breeding and migration behavior (Lindström et al. 1993a, Serra et al. 1999, Pyle 2008, Dietz et al. 2013). Despite this, few studies have quantified differences in molt duration and timing in detail for closely related species or for different groups within species. In seabirds, this is partly due to a lack of primary molt data for many species (Bridge 2006). Studying molt of flight feathers in seabirds is compromised by the fact that the birds disperse over vast expanses of ocean where collection of adequate sample sizes can be difficult. These challenges have been overcome in recent years, now that digital photography has been shown to facilitate molt scoring of flying birds (Keijl 2011, Vieira et al. 2016) and increasing numbers of photos taken during offshore surveys and opportunistic cruises are shared online.

Stercorariidae, the family of skuas and jaegers, comprises 7 species. We compared the primary molt of all 4 species of skuas and jaegers that breed in the Northern Hemisphere: Long-tailed Jaeger (*Stercorarius longicaudus*), Parasitic Jaeger (*S. parasiticus*), Pomarine Jaeger (*S. pomarinus*), and Great Skua (*S. skua*). Parasitic and Long-tailed jaegers are sister species, and evidence has been accumulating that the Pomarine Jaeger is a sister group of the Great Skua (Janssen and Mundy 2017). These species range in body mass from ~300 g in Long-tailed, ~400 g in Parasitic, and ~700 g in Pomarine jaegers to ~1,400 g in the Great Skua (Cramp and Simmons 1983). Breeding in the (sub)Arctic and spending the nonbreeding period on the oceans, all skuas are migratory, but the distances covered vary considerably between species and individuals. Nonbreeding areas vary between 50°S and 20°N in the smallest species, the Long-tailed Jaeger (Gilg et al. 2013, van Bemmelen et al. 2017), and between 10°N and 50°N in the largest species, the Great Skua (Furness 1987, Magnusdottir et al. 2012). Migration of Parasitic and Pomarine jaegers is less well studied. Pomarine Jaegers are thought to winter mainly around 0–20°N (albeit with regular occurrence to ~36°S off Australia and elsewhere), whereas Parasitic Jaegers mainly migrate to 10–50°S (Olsen and Larsson 1997, Menkhorst et al. 2017). The timing and extent of migration are thought to vary

with age and breeding success (Furness 1987). Individuals initially stay out at sea during the boreal summer of their second calendar year and may return to the breeding grounds in their third or fourth calendar years, where they arrive later in the season and remain for a shorter duration than adults (de Korte 1984, Furness 1987). Recruitment to the breeding population occurs after ≥3 yr in the Long-tailed Jaeger (de Korte 1985) and may take even longer in the other species (Furness 1987). The contrasts in body size and migration distance between species, and the contrast in the degree of migratory and breeding behavior between ages within species, allow us to explore the effect of these factors on the timing and duration of primary molt. Our expectations were that (1) larger species will require more time to renew all primaries than smaller species; (2) by starting earlier, larger species will require larger overlap with migration; (3) within a species, populations wintering farther south will have a shorter molt duration; and (4) molt duration will decrease with age as time constraints imposed by migration and breeding set in.

METHODS

Primary molt scores were obtained from several sources. Most were scored from photographs, which were either sourced from the Internet (in particular from online sighting portals), supplied by photographers, or taken by the authors. A dataset obtained in the same way and published previously by Newell et al. (2013) was also included, but all molt scores were reassessed by the first author to ascertain uniformity. Only the best visible wing was scored. Photographic records were filtered for duplicates, which could be identified by date and location, by molt status, and by individual plumage characters such as the length and shape of the central tail feathers, the amount of barring on the underparts, and the color of the head cap. Additional primary molt data were obtained from tideline corpses on Dutch beaches (Nederlandse Stookolieslachtoffer Onderzoek database), as well as from museum specimens from three sources in California, USA: the California Academy of Sciences, San Francisco (CAS); Museum of Vertebrate Zoology, Berkeley (MVZ); and Western Foundation of Vertebrate Zoology, Camarillo (WFVZ). Finally, we included published molt scores of museum specimens from Stresemann and Stresemann (1966), Lambert (1980), Melville (1983), and de Korte (1985). Individual jaegers were assigned to 4 age classes (first-cycle, second-cycle, third-cycle, and adult) representing primary molt cycles, based on plumage characters and coloration of tarsi as outlined by Howell (2007) and Pyle (2008). In Great Skuas, we only distinguished between first-cycle birds and older birds, because no reliable ageing characters are established to distinguish second- and third-

TABLE 1. Mean relative mass per primary (thus summing to 1), sample size, and the total mass of all primaries for 4 species in the family Stercorariidae as measured from dead specimens. Primaries are numbered distally, p1 being the innermost.

Species	p1	p2	p3	p4	p5	p6	p7	p8	p9	p10	Mean mass (g)	n
Long-tailed Jaeger	0.034	0.041	0.050	0.063	0.080	0.098	0.121	0.143	0.168	0.202	2.17	1
Parasitic Jaeger	0.035	0.043	0.055	0.068	0.084	0.103	0.121	0.140	0.163	0.189	3.21	4
Pomarine Jaeger	0.039	0.046	0.056	0.070	0.085	0.103	0.119	0.141	0.159	0.181	5.08	4
Great Skua	0.045	0.053	0.063	0.077	0.091	0.106	0.117	0.133	0.151	0.163	7.91	9

cycle birds from older individuals. Note that the "adult" class will include an unknown proportion of individuals that did not (yet) recruit to the breeding population, or that skipped or failed breeding in any given year.

In all 4 species, primary molt starts at the innermost primary and completes at the outermost primary (Pyle 2008). We assigned molt scores of 0 (old), 1–4 (growing and in pin or 10–33%, 33–67%, or 67–99% grown, respectively), or 5 (new and fully grown) (Ashmole 1962). Feather molt scores of 1 and 2 are usually indistinguishable in photographs (for examples, see Appendix Figure 4), because these feathers are clearly dropped but the new feathers are not yet visible beyond the primary coverts. In the case of a single invisible feather, this was scored as 1, whereas 2 invisible feathers were scored as 1 (outermost) and 2 (innermost). Fully grown primaries collected from birds found dead were cleaned, dried, and weighed to the nearest 0.001 g. Using the mean relative mass for each of the 10 primary feathers (Table 1), primary scores were converted into proportion of feather mass grown (PFMG), a molt index that increases approximately linearly over time (Summers et al. 1980). The mean relative mass of each primary reflects the shape of the wing, which shows little variation between individuals or age classes within species, but large differences between species (Dawson 2005). Indeed, the inclusion of several juveniles in our sample (1 Parasitic Jaeger, 2 Pomarine Jaegers, and 4 Great Skuas) did not affect our results. Moreover, because the relative mass of each primary (numbered p1 to p10) varied, on average, by only 2.5–4.9% within Parasitic Jaegers, Pomarine Jaegers, and Great Skuas, we considered our single Long-tailed

Skua sample to be representative for that species' wing shape.

Mean start date and duration of molt were estimated by modeling PFMG values against day since July 1 (a date that falls well outside the primary molt period in most age classes). This was done using likelihood models, referred to as UZ models (Underhill and Zucchini 1988) and implemented in the package "molt" 2.0.0 in R 3.4.0 (Erni et al. 2013, R Core Team 2017). In contrast to other methods, UZ models have specifically been designed to analyze molt data (e.g., dealing with the heteroscedasticity of molt data and biases inherent to regression methods; Summers et al. 1983, Underhill and Zucchini 1988). Only individuals in active primary molt were considered (type 3 data: Underhill and Zucchini 1988). R^2 values were obtained from linear models of observed vs. fitted values. Age was included in the models as a covariate for molt duration, starting date, and standard deviation in starting date. Given the smaller sample sizes of second- and third-cycle jaegers (Table 2), we combined these into a single age class (hereafter "second/third-cycle"). The adult age class was taken as the baseline level, because this class held the largest sample size. Optimization procedures for UZ models are sensitive to starting values (Erni et al. 2013). Therefore, convergence problems for the model of Parasitic Jaeger were solved by providing starting values, based on separate models for each molt cycle, and a standard deviation parameter of 5 days. To estimate the mean feather growth rate of adults, we divided the mean total feather mass by the estimated molt duration.

Considering the effect of nonbreeding-area latitude on molt timing and duration shown in other species (Serra et al. 1999, 2006, Underhill 2003, Pyle 2008), we also explored this by adding the covariate "latitudinal zone" for onset and duration of molt and comparing their Akaike's Information Criterion (AIC) values against models without covariates. We defined 3 latitudinal zones to investigate the potential effect of (nonbreeding-area) latitude on molt parameters: north of 35°N in the Atlantic (mainly from the North Sea or U.S. east coast) or north of 40°N in the Pacific (mainly off the U.S. west coast), from these latitudes south to the equator (mainly California Current and Canary Current), and south of the equator (mainly Australia and the

TABLE 2. Number of individuals in active primary molt per age class for 4 species in the family Stercorariidae, as used in the UZ models. No reliable plumage characteristics are known for ageing second/third-cycle Great Skuas, which are consequently included in the adult class.

	Long-tailed Jaeger	Parasitic Jaeger	Pomarine Jaeger	Great Skua
Adult	209	175	540	221
Second/third-cycle	37	53	157	–
First-cycle	32	23	88	38
Total	278	251	785	259

Benguela Current). These latitudinal zones reflect areas where jaegers normally do not spend winter, areas that can be regarded as regular "northern" nonbreeding areas and regular "southern" nonbreeding areas, respectively (Olsen and Larsson 1997).

The critical assumption of UZ models of a constant rate of change in molt index can be violated by birds that suspend molt (Underhill and Zucchini 1988, Erni et al. 2013). In molt suspension, molt is temporarily halted, to be resumed later. It results when a newer, full-grown feather falls distal to a substantially older feather, with no feathers missing (Pyle 2008, Pyle and Reid 2016; Appendix Figure 5). We expect primary molt suspension to mainly take place in birds that start molt when still well north of their nonbreeding area, suspend molt during migration, and resume after arrival at the main nonbreeding area. We therefore explored the effect of exclusion of individuals that (after being "sampled") may have suspended primary molt—those that were molting when (still) in the northern latitudinal zone—on model parameters.

In order to relate timing and duration of primary molt to migration timing, we derived individual-level timing of departure from the breeding area, arrival at and departure from the nonbreeding area, and southbound overall migration speed from light-based geolocation data for Parasitic and Long-tailed jaegers. Parasitic Jaegers were captured at Slettnes, Norway (71.0819°N, 28.2102°E; R. van Bemmelen et al. personal observation), with data spanning 3 yr (2014–2017), and Long-tailed Jaegers at Ammarnäs, Sweden (66.0048°N, 16.1842°E; van Bemmelen et al. 2017), with data spanning 4 yr (2011–2015). Both datasets were analyzed using the same techniques (for details, see van Bemmelen et al. 2017). Because both datasets span multiple years, we assume that year effects are leveled out. However, mean timing of migration for the Swedish Long-tailed Jaegers may be up to a few weeks earlier than the overall species' average, considering that breeding and migration are timed later at higher latitudes (Conklin et al. 2010), and this Swedish population is closer to the southern border of the breeding distribution. The breeding distribution of Parasitic Jaegers extends farther south (Olsen and Larsson 1997), with Slettnes taking a central position in the distribution range, and we expect that our sample therefore corresponds reasonably well with the species' overall mean migration timing. For Pomarine Jaeger and Great Skua, approximate migration periods and distances were obtained from the literature (Cramp and Simmons 1983, Furness 1987, Higgins and Davies 1996, Olsen and Larsson 1997, Magnusdottir et al. 2012) and—with the exception of geolocator data for Great Skuas (Magnusdottir et al. 2012)—are not specific to certain years or sites. We therefore assume they are generalizations over large areas and multiple years.

RESULTS

Sample Size
A sample of 1,573 individuals of Northern Hemisphere–breeding Stercorariidae was included in the UZ models, comprising 278 Long-tailed Jaegers, 251 Parasitic Jaegers, 785 Pomarine Jaegers, and 259 Great Skuas. For all species, the largest sample size was represented by the adult age class (69–85%; Table 2). Most records were obtained from photographs (98% of those for Long-tailed, 83% for Parasitic, and 86% for Pomarine jaegers; 94% for Great Skua); the remainder originated from museum specimens, except for some beached Great Skuas (3%).

Because UZ models are sensitive to outliers (Erni et al. 2013), some records that showed combinations of date and molt score not compatible with any molt cycle were removed from the dataset (prior to the above tabulation). Excluded records were as follows: (1) a first-cycle Long-tailed Jaeger on August 9, 2015, off the Scilly Islands, UK, with growing p8–9 and old p10; (2) an adult Long-tailed Jaeger sitting in poor condition on the beach in Mauritania on May 7, 2013, with p9 growing and p10 old; (3) a Long-tailed Jaeger, presumably an adult, reported on September 23, 1981, in New Zealand, with p7 growing and p8–10 old; (4) Long-tailed Jaegers picked up moribund in New Zealand during the 1982 ENSO event appeared to have delayed molt (Melville 1983), as has been shown in other seabirds (Guerra et al. 1988, Howell and Corben 2000); (5) an adult Pomarine Jaeger collected on August 1, 1967, at Barrow, Alaska, with p1–4 full-grown, p5 score 4, p6 score 2, and p7–10 old (CAS 68455); and (6) a Pomarine Jaeger on March 31, 2007, from New South Wales, Australia, showing delayed *Staffelmauser* (see below).

Staffelmauser
Five first- to second-cycle Pomarine Jaegers showed Staffelmauser (Stresemann and Stresemann 1966; Appendix Table 4), in which the second molt cycle had commenced before outer-primary replacement during the first molt was finished. Four of these, all collected in Monterey Bay, California (CAS 10932, 10965, 10979, and 11096), were duplicated to be included as both first- and second-cycle birds in the models because their PFMG values were within the range of other first- and second-cycle Pomarine Jaegers. However, a fifth Pomarine Jaeger showing Staffelmauser, photographed off New South Wales, Australia, lagged several months behind in both cycles and was excluded from the UZ models because it caused errors during model fitting. We did not find examples of Staffelmauser in the other species.

Suspended Molt
Several individuals showed suspended molt. These were 3 first-cycle (up to p7 or p8 new) and one adult (up to p9
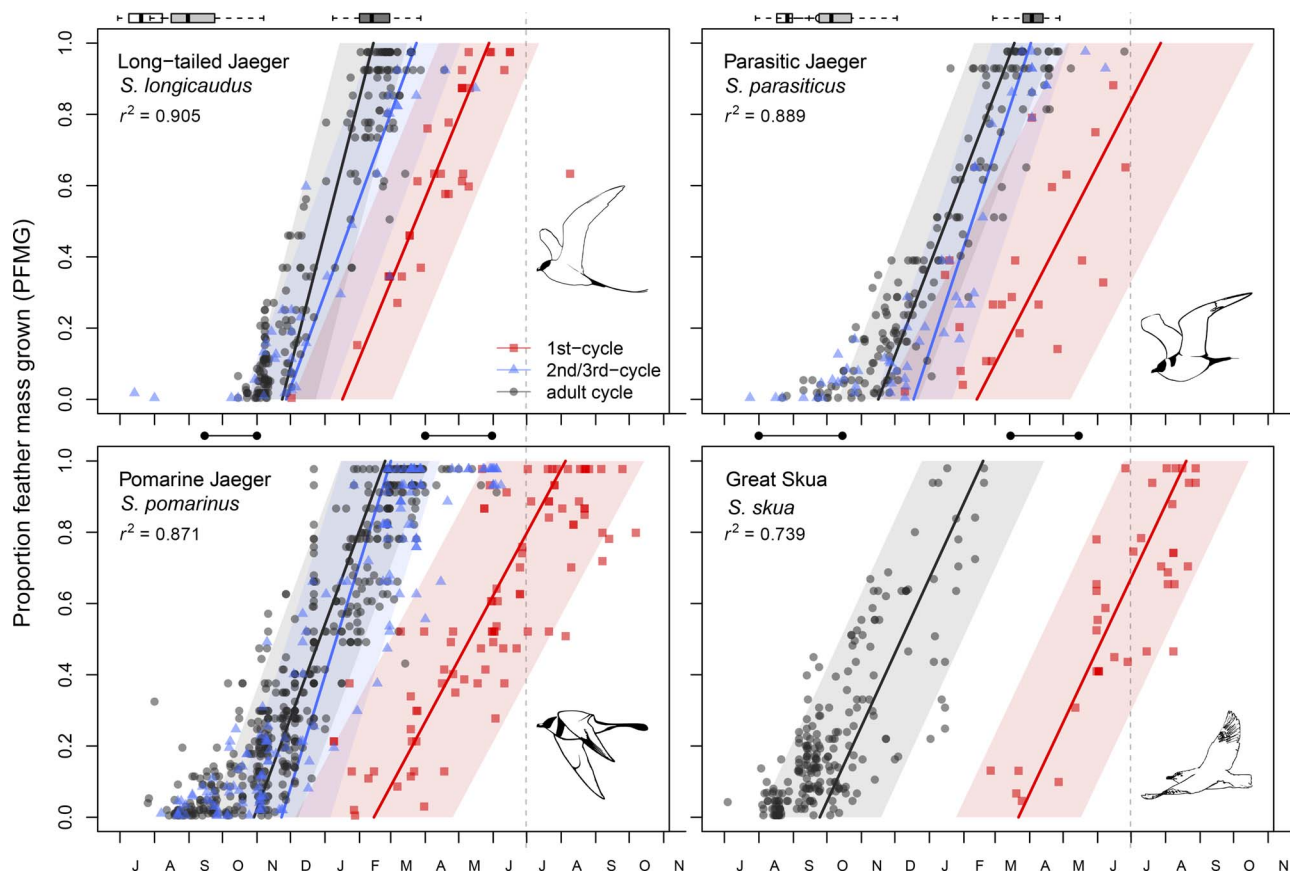
FIGURE 1. Progress of molt in adult (black), second/third-cycle (blue), and first-cycle (red) jaegers and Great Skuas, expressed as the proportion of feather mass grown (PFMG). Shaded areas represent 95% confidence intervals. Box plots above plots of Long-tailed and Parasitic jaegers show (from left to right) start of southbound migration, arrival at nonbreeding grounds, and departure from nonbreeding grounds as inferred from geolocator data. Approximate timing of migration based on the literature is shown by horizontal lines above the plots of Pomarine Jaeger and Great Skua.

new) Long-tailed Jaegers, one adult Parasitic Jaeger (only p1 new), 3 second-cycle (up to p2, p7, or p8 new) and 2 adult Pomarine Jaegers (up to p1 and p2 new), and a single adult Great Skua (up to p9 new). We may have missed suspended molt in other records, given that the detection depends on the quality of the picture and the difference in age of old and new feathers.

Model Results

All 4 species display clear temporal patterns in molt timing. Among adults, Great Skuas showed the longest molt duration and Long-tailed Jaegers the shortest (Figures 1 and 2; Table 3). However, the molt durations of Pomarine and Parasitic jaegers were virtually the same, despite the distinctly larger size of the former. Projected end dates for adults were February 13 for Long-tailed Jaegers, March 18 for Parasitic Jaegers, February 23 for Pomarine Jaegers, and February 18 for Great Skuas. The molt of first-cycle birds was well separated in time from that of the adults, as well as from second/third-cycle

birds, and this timing difference increased with species' body weight. In the 3 jaeger species, molt took considerably longer in first-cycle birds than in adults (longer by 50, 43, and 54 days); while in Great Skuas, molt duration was similar between those two age classes (4 days longer in first-cycle birds). Duration of molt in second/third-cycle birds was more or less similar to that of adults. The model outputs suggest that second/third-cycle Long-tailed Jaegers start at the same time as adults but have a 35-day-longer molt duration, whereas second/third-cycle Parasitic and Pomarine jaegers have a molt duration that is shorter than that of adults by 17 and 20 days, respectively. All models had very high R^2 values.

Adults were the only age class with sufficient data from separate latitudinal zones to test for the effect of latitude. The distribution of records of adults among the 3 latitudinal zones was as follows, from north to south: 0, 65, and 144 Long-tailed Jaegers; 13, 43, and 119 Parasitic Jaegers; 22, 275, and 243 Pomarine Jaegers; and 213, 8, and 0 Great Skuas. For all 3 jaeger species, adding "latitudinal
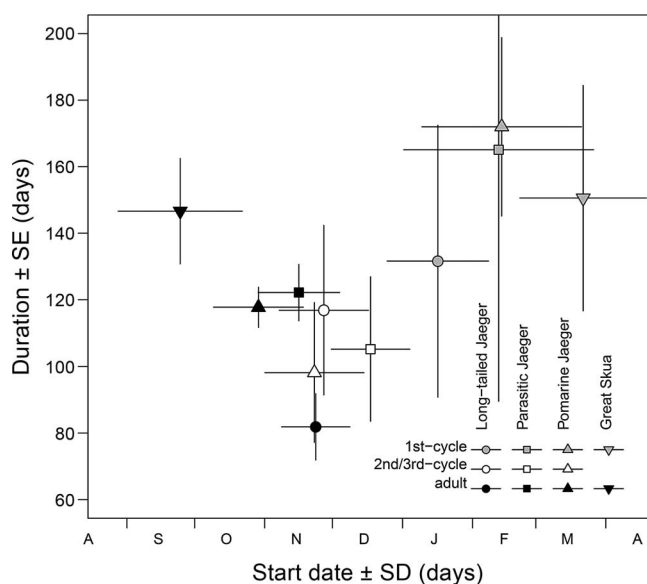
FIGURE 2. Parameter estimates for starting date (x-axis) and molt duration (y-axis) for adult, second/third-cycle, and first-cycle jaegers and Great Skuas. Note that the upper SE of first-cycle Parasitic Jaeger extends beyond the bounds of the figure.

zone" did not result in large decreases of AIC values (ΔAIC > -2) compared to UZ models without covariates.

We found no apparent effects related to Parasitic and Pomarine jaegers that may have suspended molt after being sampled. Removal of samples from the northern latitudinal zone had only a small effect on molt duration (<0.4 days) and on mean starting date (<2 days) in both species. We could not perform this analysis for Long-tailed Jaegers, given the lack of molting adults in the northern latitudinal zone, or for Great Skuas, which largely remain within the latitudinal zone. In addition, we could not repeat this analysis for first-cycle or second/third-cycle datasets, because of smaller sample size.

Migration

Timings of departure from the breeding areas, and arrival at and departure from the nonbreeding areas, are reported for Parasitic and Long-tailed jaegers in Figure 1. Parasitic

and Long-tailed jaegers traveled, on average, 273 km day^{-1} ($n = 29$) and 293 km day^{-1}, respectively ($n = 60$). According to the literature, Great Skuas breeding in Scotland complete a migration of 3,000–3,500 km to Iberia or northwest Africa (based on light-level geolocator data in Magnusdottir et al. 2012) in $\sim$2 mo (Cramp and Simmons 1983, Furness 1987). This suggests they travel approximately 50–60 km day^{-1}.

DISCUSSION

Consistent with our expectations, we found that molt of primaries in the larger Great Skua generally took longer, started earlier, and had a larger temporal overlap with migration than in the 3 jaeger species. Within jaeger species, differences in molt duration between age classes suggest time constraints to finish molt before northward migration. While these findings are largely in line with previous publications (Olsen and Larsson 1997, Wiley and Lee 1998, Howell 2007, 2010, Pyle 2008, Pyle and Reid 2016), we provide more precise estimates of molt onset and duration and a uniform data analysis for all 4 species and identifiable age classes, allowing interspecific and intraspecific comparisons.

Molt durations of adult Parasitic and Pomarine jaegers were surprisingly similar, given that they differ significantly in body weight (335–470 vs. 542–917 g, respectively; Cramp and Simmons 1983). A longer molt duration in Parasitic Jaegers, approximating that of Pomarine Jaegers, is difficult to explain. Molt suspension may lead UZ models to overestimate the duration of active molt, but models of both species appeared to be robust to the inclusion of individuals that may have suspended molt after being sampled. Another possible modeling issue would be a poor model fit due to covariance of molt parameters, which is a known problem for type 3 UZ models (Underhill and Zucchini 1988, Erni et al. 2013). Although this was the case in models for both Parasitic ($r = -0.897$) and Pomarine ($r = -0.912$) jaegers, we can see no reason why this would affect the models for the 2 species differently.

TABLE 3. Model estimates for mean start date and duration (days) of primary molt in 4 species in the family Stercorariidae. In parentheses, SD values are indicated for the mean start date and SE values for molt duration. For sample size per species and age class, see Table 2. Parameters are missing for second/third-cycle Great Skuas because no reliable characters are known to distinguish these age classes from older birds.

| Species	First-cycle		Second/third-cycle		Adult		R^2
	Start date	Duration	Start date	Duration	Start date	Duration	
Long-tailed Jaeger	January 16 ($\pm$ 22)	132 ($\pm$ 41)	November 27 ($\pm$ 22)	117 ($\pm$ 25)	November 23 ($\pm$ 15)	82 ($\pm$ 10)	0.905
Parasitic Jaeger	February 12 ($\pm$ 42)	165 ($\pm$ 76)	December 17 ($\pm$ 42)	105 ($\pm$ 22)	November 16 ($\pm$ 18)	122 ($\pm$ 8)	0.889
Pomarine Jaeger	February 13 ($\pm$ 35)	172 ($\pm$ 27)	November 23 ($\pm$ 35)	98 ($\pm$ 21)	October 29 ($\pm$ 20)	118 ($\pm$ 6)	0.871
Great Skua	March 21 ($\pm$ 28)	151 ($\pm$ 34)	–	–	September 24 ($\pm$ 27)	147 ($\pm$ 16)	0.739
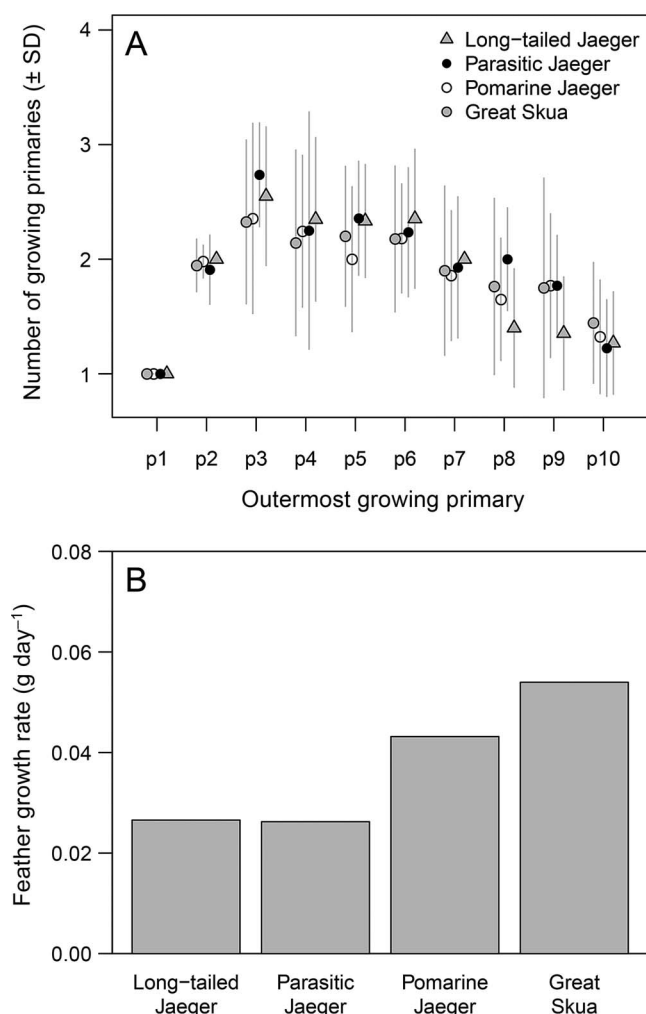
FIGURE 3. (**A**) Molt intensity (number of primaries growing simultaneously) throughout the molt (upper panel) and (**B**) deduced mean feather growth rate (lower panel) in adults of 4 species in the family Stercorariidae.

Alternatively, model results could reflect a true similarity in molt duration between Parasitic and Pomarine jaegers. Molt duration is determined by both the number of simultaneously growing feathers (molt intensity) and the time required to grow individual feathers (growth rate). While total feather mass is clearly larger in Pomarine Jaegers (Table 1), molt intensity was not different between the 2 species at any time during primary molt (Figure 3), which suggests that feather growth rate (grams per day) could explain the similar molt durations. Given that feather growth rate tends to increase with body mass in birds (Rohwer and Rohwer 2013), we expected the Parasitic Jaeger's feather growth rate to be intermediate between those of Long-tailed and Pomarine jaegers, but in fact it was surprisingly similar to that of the former and lower than that of the latter (Figure 3). Thus, Parasitic Jaegers may arrive at a molt duration similar to that of

Pomarine Jaegers by a relatively low feather growth rate. This would be remarkable, given that the predominant strategy for adjusting molt duration in birds is by modifying molt intensity rather than feather growth rate (Rohwer and Rohwer 2013). The benefit of decreasing feather growth rate could be higher feather quality, given that shortening molt duration has been shown to decrease feather quality (Dawson et al. 2000, Serra 2001). High feather quality may be especially important in Parasitic Jaegers to avoid feather damage when performing frantic aerial pursuits of terns and other seabirds.

In addition to the effect of body size on molt duration (Rohwer et al. 2009), time costs of migration may have an additive effect leading to shorter molts (De la Hera et al. 2009). This may result from "squeezing in" the molt between breeding and postbreeding migration, but when molt is postponed to the wintering period—as in our study species—shorter molts may result from less time spent at the wintering grounds due to longer migration durations. Although Great Skua indeed has the shortest migration distance and the longest molt duration, the pattern does not hold for jaegers; the Pomarine Jaeger has the shortest winter period and the Long-tailed Jaeger the longest, but molt duration is shorter for the latter. Moreover, we expected any effect of migration distance on molt duration also to be reflected within species, but this was not the case; molt duration in all 3 jaegers did not differ significantly between areas north and south of the equator.

Previous studies indicated that shorebirds and procellariiform seabirds that migrate to the tropics or the Southern Hemisphere display longer molt durations than observed in related migratory species or populations of the same species that remain in the Northern Hemisphere (Serra et al. 1999, 2006, Underhill 2003, Pyle 2008). Birds that remain in the Northern Hemisphere appear to be under greater time constraints to complete molt before the onset of winter conditions, with fewer resources, less favorable weather, and reduced daylight in which to forage. Our results did not reveal such a latitudinal difference between (1) subtropical areas north and (2) subtropical to temperate areas south of the equator, despite differences in, for example, day length. Jaegers that remain in northern temperate waters during the nonbreeding period (which is uncommon in Pomarine, rare in Parasitic, and extremely rare in Long-tailed jaegers; Olsen and Larsson 1997) may face time constraints, but our samples from this region were too small to robustly estimate the timing and duration of primary molt in these waters. Similarly, it would be interesting to test for a difference in molt duration between Great Skuas from the present study that probably wintered off Africa and Iberia and those wintering in the Grand Banks area near Newfoundland, Canada (Magnusdottir et al. 2012).

Among our study species, larger species started molt earlier, thereby creating a temporal overlap of primary molt and southbound migration. Migratory bird species usually molt before or after migration, or divide molt between these periods. In the latter case, molt can be suspended during active migration, which means that no wing surface gap is present. In the smallest species in the Stercorariidae, the Long-tailed Jaeger, we found neither adults that suspended molt in the inner primaries nor birds of any age class that started primary molt well north of the nonbreeding areas and could have suspended molt later on. In the Parasitic Jaeger, starting primary molt in northern temperate regions seems an uncommon strategy. Only a few of the molting adults in our data were from northern temperate areas, and all were photographed in September–October and in early molt; one adult from Monterey Bay, California, USA, had suspended molt after growing the innermost primary (MVZ 101196). In line with this, Olsen and Larsson (1997) state that 5% of Parasitic Jaegers start primary molt in temperate waters. Some of these adults may stay throughout the nonbreeding area in northern temperate waters instead of the usual tropical or southern temperate nonbreeding areas. Pomarine Jaegers start postbreeding migration later than Parasitic Jaegers and are commonly encountered in early primary molt off central California. Here, they become much scarcer later in the boreal winter (Briggs et al. 1987), which suggests that birds that have begun molt move southward later on. Individuals may then suspend molt at p1 or p2 during migration, as indicated by 2 adult specimens from Monterey Bay, California, USA (MVZ 17765 and 17800). Thus, both Parasitic and Pomarine jaegers can suspend molt during southbound migration, but whether some individuals migrate with molt gaps remains unknown.

By contrast, our results indicate a complete overlap of migration with primary molt in Great Skuas. Great Skuas start primary molt at or directly after departure from the breeding grounds (Cramp and Simmons 1983, Furness 1987). Data collected at Jan Mayen and included in our study indicate that, in pairs with chicks close to fledging, at least one of the partners had dropped the inner primary. Molt then continues during southbound migration. In November–December, when adult Great Skuas are virtually absent from the North Sea (Camphuysen and Leopold 1994, Furness et al. 2006) and have moved farther south and west, molt has progressed only halfway. Such an extensive overlap of molt and migration is usually considered rare among migratory birds, but less rare among short-distance migrants and species that feed on the wing, such as terns and hirundines (Yuri and Rohwer 1997, Zenatello et al. 2002). It is not clear to what extent other seabird species molt primaries during migration, but at least some albatross species may cover huge distances

while actively molting (Croxall et al. 2005). In albatrosses, this may be facilitated by a low molt intensity, thereby minimizing the molt gap and negative effects on flight performance (Prince et al. 1993). Great Skuas, however, can have substantial molt gaps. Rather, molt-migration overlap in Great Skuas may be facilitated by a short migration distance and low travel speeds. Indeed, Parasitic and Long-tailed jaegers travel $\sim$300 km day^{-1}, whereas Great Skuas breeding in Scotland travel at only $\sim$50 km day^{-1}. In fact, travel speed in Great Skuas is so low that one could argue they are more or less stationary most of the time. In addition to travel speeds, high food availability en route may facilitate molt-migration overlap in Great Skuas migrating through productive waters of the North Sea and Gulf of Biscay. By contrast, while migrating between staging in productive areas, jaegers move fast over unproductive subtropical and tropical waters from the central North to the South Atlantic (e.g., van Bemmelen et al. 2017), where molt may need to be postponed or suspended not only because of food limitation. Time constraints, and the need of waterbird species that remain in the Northern Hemisphere for the nonbreeding season to complete molt more quickly than species that occupy more southerly nonbreeding areas, may also affect the degree to which jaegers and skuas undergo active primary molt during migration (Pyle 2008).

Although mean starting dates of adults differed by 2 mo, Long-tailed Jaegers, Pomarine Jaegers, and Great Skuas finished within 10 days of each other, whereas Parasitic Jaegers finished 23 days later. These mean end dates, from late January through early March, are just before the onset of northbound migration as inferred from geolocator data and literature. We found no evidence of molt-migration overlap in the period January–May, in contrast to individuals in active molt during southbound migration at northern temperate latitudes. Our interpretation is therefore that individuals start northbound migrating only after they have finished primary molt. Among migratory birds breeding in the Northern Hemisphere, migration speed is usually higher during northbound than during southbound migration, indicating a high selection pressure for timely and fast migration (Nilsson et al. 2013). Conceivably, overlap of molt with northbound (prebreeding) migration entails larger costs than overlap with southbound (postbreeding) migration. For example, the elevated energy requirements (Lindström et al. 1993b) and decreased flight performance (Hedenström and Sunada 1999) of molt may constrain migration speed and lead to later arrival in the breeding area (Gorney and Yom-Tov 2001), which can affect breeding performance (Harrison et al. 2011).

The absence of molt-migration overlap during northbound migration and the (nearly) coinciding dates of molt completion and departure from the nonbreeding areas

(Figure 1) suggest that molt in adults is timed to finish just prior to northbound migration. That this reflects a time constraint is suggested by the ∼50 days longer molt duration and larger variation in starting dates of first-cycle jaegers compared to adults (Pyle 2008, Howell 2010). Unlike adults, first-cycle jaegers are not constrained by breeding duties or migration back to the breeding areas. Shorter primary molt duration of adults compared to first-cycle individuals has also been reported in two other Arctic-breeding, long-distance migrants, the Black-bellied Plover (*Pluvialis squatarola*) and the Red Knot (*Calidris canutus*), in which second-calendar-year individuals do not breed and usually remain on the nonbreeding grounds during the boreal summer (Serra et al. 1999, Dietz et al. 2013). In contrast, most second-calendar-year Wood Sandpipers (*Tringa glareola*) migrate north directly after an incomplete primary molt on the nonbreeding grounds, and this molt takes as long as that of adults (Remisiewicz et al. 2010). An alternative or additional reason for a longer molt duration in first-cycle jaegers may be primary molt suspension, which was observed in some first-cycle Long-tailed Jaegers (Pyle and Reid 2016) and also may explain first-cycle Long-tailed Jaegers being in active primary molt in the (late) boreal summer (Wiley and Lee 1998) or even Pomarine Jaegers showing Staffelmauser. Potentially, first-cycle jaegers might suspend primary molt during a (poorly known) northbound migration. Their rarity at the breeding areas during the boreal summer suggests that they usually do not migrate all the way to the Arctic (de Korte 1984, van Bemmelen 2010), and first-cycle birds are apparently absent from the Benguela nonbreeding areas during the same period (Lambert 1980), which suggests that most stay in tropical or temperate waters (Howell 2010). Finally, first-cycle jaegers may be constrained by lower foraging success due to less experience or exclusion from high-quality habitats. However, these options remain speculative until the movements of younger jaegers are uncovered. In contrast to the 3 jaeger species, molt duration and variation in starting date were virtually equal in first-cycle and older Great Skuas, despite similar contrasts between age classes in breeding and migration as in the jaegers. Adult Great Skuas may have compensated for the time constraint by a greater overlap of molt with southbound migration.

We also expected a longer molt duration in second/third-cycle jaegers than in adults, but our results were inconclusive. We found a longer duration in second/third-cycle than in adult Long-tailed Jaegers, and shorter durations for Parasitic and Pomarine jaegers. Again, covariance between the parameters for duration and onset of molt may have led to underestimated durations for Parasitic and Pomarine jaegers. Alternatively, second/third-cycle Parasitic and Pomarine jaegers already face similar time constraints as adults if they are migrating to the Northern Hemisphere breeding area. However, this should also have been reflected in Long-tailed Jaegers: third-calendar-year birds (thus between the second and third cycles) of this species are regularly recorded at the breeding grounds (de Korte 1984, van Bemmelen 2010).

The molt parameters presented here can inform us when specific primaries are molted, which is critical information for study design and data interpretation when sampling biomarkers from primaries. This applies not only to future studies, but also to reinterpretation of published results. For example, Furness et al. (2006) reported a gradual change through p1 to p10 in both $\delta^{15}N$ and $\delta^{13}C$ stable isotopes in Great Skuas and suggested that this reflected a gradual change in diet to lower trophic levels. However, given that Great Skuas actively molt during migration, an alternative explanation is that this merely reflects the environmental gradients in stable isotope ratios over which Great Skuas traverse. Indeed, isoscapes published after Furness et al. (2006) show gradients in stable isotope ratios of both elements in near-surface plankton along the Great Skua's migration route (Graham et al. 2010), which is expected to be reflected in higher trophic levels, including within the growing feathers of top predators such as the Great Skua. Given that the smaller species also may move during primary molt (van Bemmelen et al. 2017), we suggest sampling several primaries to obtain biomarker signals along molting locations.

The present study is one of only a few that have used digital photographs to obtain avian molt data (Keijl 2011, Conklin and Battley 2012, Vieira et al. 2016). We gathered these largely from the Internet. With the increase in popularity of (pelagic) birding, digital photography, and the ever-increasing capacity to share large numbers of observations and images on the Internet, we consider this approach to have great potential for the study of molt in other seabird species. There is a clear need for such studies, given the increasing use of biomarkers sampled from flight feathers and other feather tracts, while adequate molt data remain lacking for many species (Bridge 2006, 2011).

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APPENDIX TABLE 4. Details of Pomarine Jaegers showing Staffelmauser (see text). PFMG (proportion of feather mass grown) values for the first cycle (the molt wave that has advanced farther toward the outer primaries) are calculated by setting new growing feathers of the second molt cycle (inner primaries) to 5 (fully grown), whereas those grown or growing in the first cycle are set to 0 (old) to calculate PFMG values for the second cycle.

Specimen	Date	Location	Molt score	PFMG First cycle	PFMG Second cycle
CAS-10932	August 1, 1907	Monterey Bay, CA, USA	2155555554	0.977	0.011
CAS-10979	September 25, 1907	Monterey Bay, CA, USA	3155555554	0.977	0.030
CAS-11096	August 22, 1907	Monterey Bay, CA, USA	2155555542	0.867	0.011
CAS-10965	August 22, 1907	Monterey Bay, CA, USA	1555555554	0.997	0.005
	March 31, 2007	New South Wales, Australia	5515555420	0.701	0.092

APPENDIX FIGURE 4. Adult Pomarine Jaeger in active primary molt, off Mauritania on November 11, 2016. Primary molt was scored as 5542100000, resulting in a PFMG value of 0.171. Note that p4–5 are invisible and scores for these feathers were inferred. Photo credit: Rob van Bemmelen

APPENDIX FIGURE 5. Second-cycle Pomarine Jaeger that suspended molt after growing p1–2, off Wollongong, New South Wales, Australia, October 23, 2010. Photo credit: Raja Stephenson