ORIGINAL PAPER

Prebasic molt initiation and progress in northern fulmars of the High Arctic: do molt and breeding overlap?

Karel A. Allard · Mark L. Mallory · Kerrie L. Wilcox · Mark R. Forbes

Abstract We examined feather molt progress of northern fulmars (*Fulmarus glacialis*) at Cape Vera in the Canadian High Arctic through opportunistic observation of individuals in flight from 2003 to 2006, and examination of bodies and wings of 127 individuals collected at the site, from 2003 to 2005. We found no evidence suggesting that fulmars shed primary feathers during breeding. Prebasic molt was initiated in the head, neck, sides, belly and back approximately 1 week before hatch. We failed to detect a sex effect on molt progress, but molt among breeders was delayed compared to molt in non- or failed breeders. This study constitutes a baseline we feel may be useful to: (1) researchers interested in feather replacement chronology, wherein feathers are used as sources of biological information; and (2) researchers interested in eventual assessment of relationships among large-scale environmental processes and molt progress in this species, especially in light of predicted changes to Arctic regions.

Keywords Northern fulmar · *Fulmarus glacialis* · Molt · Primary feather · Arctic

K. A. Allard
ACWERN, Biology Department,
University of New Brunswick,
PO Box 45111, Fredericton,
NB, Canada E3B 6E1

M. L. Mallory (✉)
Canadian Wildlife Service,
Box 1714, Iqaluit, NT, Canada X0A 0H0
e-mail: mark.mallory@ec.gc.ca

M. L. Mallory · M. R. Forbes
Department of Biology,
Carleton University,
Ottawa, ON, Canada K1S 5B6

K. L. Wilcox
Avian Energetics Laboratory,
Long Point Waterfowl and Wetlands Research Fund,
Bird Studies Canada, 115 Front Street, Port Rowan,
ON, Canada N0E 1M0

Introduction

Characteristics of local breeding bird populations, such as timing of breeding, measures of body condition and their proxies, as well as reproductive output in birds, are commonly proposed metrics valuable to investigation of ecological change (e.g., Visser et al. 1998; Frederiksen et al. 2004; Grosbois and Thompson 2005). More recently, increasing numbers of studies use tissues, including feathers, as source material (e.g., work with isotopes) to infer on contaminant burden, diet and geographical distribution within and among species (e.g., Hodum and Hobson 2000). Studies which use feathers in particular rely on knowledge of molt chronology (e.g., Thompson and Furness 1995), often derived from the literature, and are vulnerable to poorly understood potential sources of variation. Also, molt strategies and variation in molt progress (i.e., timing of onset, and rate) often are overlooked and remain largely understudied (Ginn and Melville 1983). Molt, reproduction, migration, and the accumulation of fat reserves are considered energetically-demanding processes for birds (Chu 1984; King and Murphy 1985), and tend to be temporally segregated and timed with periods of food abundance (Payne 1972; Ricklefs 1974). For example, molt of flight feathers and reproduction generally occur at different times, likely to optimise the trade-off between breeding success and survival until the next breeding season (Holmgren and Hedenström 1995; Robertson et al. 1998). Though molt can

represent a relatively small net daily expenditure in terms of feather synthesis (King and Murphy 1985; Norstrom et al. 1986), additional costs might also be incurred through reduced flying ability (Beck 1970; Swaddle and Witter 1997; Lindström et al. 1994) and reduced foraging efficiency, as well as increased thermoregulatory expenses. According to theory, costs incurred through increased energetic expenditures related to molt would compete with allocation of resources to reproductive effort, and thus selection should favour molt initiation occurring upon completion of breeding.

In some situations, however, where food resources are not limiting, or environmental conditions place constraints on the completion of other life history processes (e.g., migration), molt and breeding may overlap (reviewed by Bridge 2006). For example, Barbraud and Chastel (1998) showed that southern fulmars (*Fulmarus glacialoides*) breeding in Antarctica initiated primary molt during incubation, presumably due to a short summer season and abundant marine food supplies, and a similar explanation was proposed for molt-breeding overlap in giant petrels (*Macronectes* spp.; Hunter 1984). Furthermore, the absence or removal of costs of breeding should lead to earlier onset of molt for failed breeders, non-breeding adults and juveniles, which has been observed in many species (Ginn and Melville 1983).

We studied molt in northern fulmars (*Fulmarus glacialis*), the only petrel (Procellariiformes) found in the Boreal, Low Arctic and High Arctic oceanographic zones (Salomonsen 1965). The timing of molt and reproduction typically are segregated in the petrels (Warham 1996), including fulmars (Hatch 1979; Hatch and Nettleship 1998), although Bridge (2006) recently suggested that that Procellariiformes were more likely to overlap molt and reproduction than other seabirds, especially in sedentary or dispersive populations. Fulmars undergo a single, complete molt (Hatch and Nettleship 1998), the timing of which varies primarily in relation to breeding status. Non-breeders enter molt earlier than breeders, and primary molt is initiated by failed breeders approximately 2 weeks after nest loss (Hatch and Nettleship 1998). However, many earlier studies of molt in this and other species failed to distinguish effectively breeders from non- or failed breeders. Furthermore, incorrectly qualifying failed or non- breeders as breeders can lead to the false conclusion that overlap exists between molt and reproduction. This stresses the importance of individual-based information in molt studies and the challenge inherent to comparison with some earlier studies. Molt has been documented in fulmars principally occupying colonies in the Boreal oceanographic zone (Duffey 1950; Carrick and Dunnet 1954; Dott 1973; Hatch 1979). Body molt in breeding individuals at Alaskan colonies was observed as early as late incubation, with onset of primary molt occurring rarely near the end of chick-rearing (Hatch 1979; Hatch and Nettleship 1998). The observation that some breeders initiate primary molt in late incubation

(Hatch 1979) might be attributable to high food resource abundance (Carrick and Dunnet 1954).

We observed molt by fulmars breeding at the remote Cape Vera colony in the Canadian High Arctic (Mallory and Fontaine 2004) and assessed molt progress at both the individual and colony levels, to compare to these previous studies. Little information on molt chronology exists for the large fulmar populations associated with colonies in this region, except for some observations of molting fulmars at sea (Brown 1988; data available at http://seamap.env.duke.edu). Polar regions are characterized by having: (1) shortened seasonal opportunities for reproduction; (2) extreme winter conditions and sea-ice cover which collectively impose the need to migrate; and (3) spatially and temporally concentrated food resources (Hamer et al. 2002). At Cape Vera, fulmars exhibit a compressed and adjusted breeding schedule and relatively long incubation shifts (Hatch and Nettleship 1998; Gaston et al. 2005), which presumably reflect behavioral adaptations to low marine productivity (i.e., food supplies) during the early part of the breeding season (Raymont 1976).

The principal objectives of this study on northern fulmars in the Canadian High Arctic were to: (1) establish the first baseline chronology of body molt for this region; (2) determine whether incubation and molt overlap, as seen for southern fulmars (Barbraud and Chastel 1998); (3) assess how molt differs among breeders and non-breeders; and (4) determine whether there are sex-specific differences in molt patterns.

Materials and methods

The study was undertaken at Cape Vera, Devon Island, Nunavut, Canada (76°15′N, 89°15′W) where 71, 32, and 24 individual fulmars were collected during 2003, 2004, and 2005, respectively, as part of a larger project examining the ecology of fulmars at this remote site. The 2003 sample included breeders, failed breeders and likely non-breeders captured between 10 June and 18 August. The remaining fulmars were breeders collected 18 May and 16 July 2004, and 4 May and 11 June 2005, respectively. Birds were captured on the nest using poles equipped with nooses, and were quickly euthanized by decapitation. Those birds captured during pre-laying were assumed to be breeders (Mallory and Forbes 2007), while those captured after egg-laying were classed as breeders if they were incubating an egg. The 2003 sample also included individuals shot with shotguns in the vicinity of the colony (following Canadian Council on Animal Care guidelines). These birds were principally non- or failed breeders, based on telemetry work conducted at the site (Mallory, unpublished data), as well as information from dissection (below). Fulmars varied in color from dark (DD) to light (LL), although the majority were in the intermediate categories (D and L; Hatch and Nettleship

1998). Carcasses were fully examined in a suite of studies including diet, contaminants (Mallory et al. 2006a), marine pollution, body condition, parasitology (Mallory et al. 2006b), haematology (Edwards et al. 2005), and morphometry (Mallory and Forbes 2005).

All birds sampled were sexed through dissection and direct examination of gonads. Presence and size of a post-ovulatory follicle, determined through dissection, allowed us to classify further females as non- versus failed breeders. Also, telemetry evidence suggests breeders leave the colony to forage hundreds of kilometers to the east (Mallory, unpublished data), thereby spending less time at or near the colony shoreline area. We were otherwise unable to age individuals. Northern fulmars at the site exhibited high breeding synchrony, thus limiting the utility of correcting for differences in breeding phenology among individuals (i.e. number of days after clutch initiation), a potentially important covariate in other circumstances and in other species.

We determined intensity of feather replacement through counts of blood quills in 20 feather regions (Titman et al. 1990; Thompson and Drobney 1995): crown, cheek, chin–throat, neck, upper back, scapulars, lower back, rump, upper tail coverts, rectrices, undertail coverts, collar, breast, belly, side, flank, primaries, secondaries, tertials, and wing coverts (Petrie 1998). Each feather region was subject to three grab samples. Molt intensity initially was obtained by calculating a percentage of the number of pin and/or growing feathers compared to completed molted feathers within each of the 20 individual regions. For each individual, we then calculated a mean total molt intensity value which represented the mean of all feather region molt intensities, with values of 0 representing no molt, 0.01–1.0 representing light molt, and values ≥ 1.01 representing intermediate or heavy molt (Thompson and Drobney 1995).

We used the method of Ashmole (1962) to obtain primary molt scores (PMS), calculated as the sum of molt scores obtained from each primary feather (0, old feather in place; to 5, new feather fully grown), from innermost P1 to outermost P10, in each wing. Although primary molt typically is thought to be symmetrical (Weimerskirch 1991), we examined and calculated molt scores for both right and left wings. Also, from 2003 to 2006, through the breeding season we recorded opportunistically the proportion of flying fulmars observed in primary wing molt, by counting at least 100 birds at one viewing each day, and recording how many of those birds exhibited wing molt. We conducted the same procedure at a separate fulmar colony (Prince Leopold Island, 74°N, 90°W) in 2005.

Statistical analyses

We used paired t tests, Mann–Whitney U tests, Kruskal–Wallis tests, and Fisher's Exact tests to assess possible differences in molt symmetry between sexes, breeding status, or months, or to compare proportions of molting birds. An ANCOVA was used to test for differences in primary molt scores between sexes, with sex as a main effect and date of collection as a covariate. Trends in proportion of birds exhibiting primary molt were assessed using Pearson correlation. All dates were converted to Ordinal Dates (1 January = 001) for analysis. Means are reported $\pm$ SE, and all tests were two-tailed and use a significance level of 0.05 (Systat Software Inc. 2002).

Results

Breeding chronology

The timing of breeding was consistent among years, with mean date of egg-laying occurring on 6 June in 2004 (Ordinal Date 157.1 $\pm$ 0.6, $n = 16$) and 2005 (157.9 $\pm$ 0.2, $n = 103$).

Wing molt

Pooling data from 3 years, 71 breeding adults were captured on the colony between nine and 83 days prior to the median hatch date at the colony (i.e., pre-laying through 66% of incubation). Of these, none (0%) showed any evidence of wing feather molt in primary, secondary, tertiary, axillary, or alulae regions, including inner and outer wing coverts (Table 1). We did not collect any known breeders later in the season, but we observed no primary molt in 47 adults provisioning chicks during 1–14 August 2003. In contrast, non- or failed breeders in 2003 exhibited molt in various wing feather regions. During August, an average of 36 $\pm$ 4 of 100 birds observed at the shoreline were in obvious primary molt, a significantly higher proportion than among confirmed breeders (Fisher Exact test, $P < 0.0001$).

The proportion of fulmars exhibiting primary wing molt increased through the breeding season (Fig. 1), both at Cape Vera ($r_{67} = 0.88$, $P < 0.001$) and Prince Leopold Island ($r_{38} = 0.88$, $P < 0.001$). Fulmars were first observed losing primary feathers on day 174 (23 June), approximately 2 weeks after the mean egg-laying date for the colony. The proportion of birds observed in primary molt between 14 and 19 July was similar each year: 2003—12%, 2004—13%, 2005—12%, 2006—16% ($KW = 1.4$, $P = 0.7$). Peak counts of molters, averaging 43% of birds observed at the shoreline, occurred between day 223 and 226 (11–14 August), although we cannot exclude the possibility that higher proportions occurred after this date, as our observations ended then.

Individuals observed flying along the breeding cliffs near the mean hatch date for the colony were less likely to show signs of molt than conspecifics observed flying along the

Table 1 Mean (SE) percentage of molt intensity of 20 feather regions from northern fulmars collected during the breeding seasons of 2003–2005 at Cape Vera, Nunavut, Canada

Feather tract	Breeders		Non- or failed breeders	
	Male (35)	Female (29)	Male (23)	Female (23)
Crown	0	0	0.1 (0.1)	1.4 (0.6)
Cheek	0	0	0.9 (0.6)	5.5 (2.4)
Chin/throat	0	0	1.0 (0.7)	2.6 (2.0)
Neck	0.1 (0.1)	0.1 (0.1)	0.6 (0.4)	3.4 (1.6)
Upper back	0.6 (0.4)	0.1 (0.1)	2.1 (1.1)	3.4 (1.4)
Scapulars	0.1 (0.1)	0	1.7 (0.9)	4.5 (1.9)
Lower back	0.8 (0.6)	0	1.4 (1.0)	3.4 (1.3)
Rump	0.3 (0.3)	0	1.3 (0.9)	5.9 (2.4)
Upper tail coverts	0.7 (0.5)	0	0.5 (0.5)	3.3 (1.6)
Rectrices	0	0	0	1.2 (1.2)
Undertail coverts	0	0	1.8 (1.2)	2.1 (1.0)
Collar	0.9 (0.6)	0	0.3 (0.3)	3.8 (1.8)
Breast	0.04 (0.04)	0	0.5 (0.5)	0.02 (0.02)
Belly	0.1 (0.1)	0	0.3 (0.3)	0.2 (0.2)
Side	0.8 (0.5)	0	0.4 (0.3)	0.7 (0.7)
Flank	1.6 (1.3)	0.3 (0.3)	0	0.4 (0.4)
Primaries	0	0	19.6 (3.7)	27.8 (3.7)
Secondaries	0	0	0.7 (0.4)	1.6 (0.8)
Tertials	0	0	42.0 (9.4)	47.8 (9.8)
Wing coverts	0	0	0.3 (0.2)	1.8 (0.9)
Total molt score	0.05 (0.03)	0.03 (0.02)	0.22 (0.04)	0.40 (0.06)

Only birds with complete data for all feather regions are included. Inferences should not be drawn from comparisons between breeders and non- or failed breeders
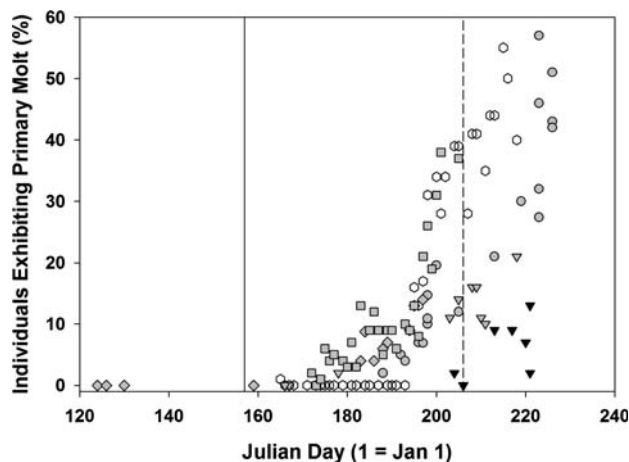
Fig. 1 Sampled proportions of 11,500 individuals in flight exhibiting primary molt. Each point represents a sample of 100 birds observed from either a colony or shoreline position. Points differ by year and location as follows: (1) Cape Vera 2003 (*filled circles*), 2004 (*filled triangles*; *black* are counts made from the cliffs), 2005 (*filled diamonds*), 2006 (*filled squares*); (2) Prince Leopold Island 2005 (*open circles*)

shoreline away from the colony (≥ 1 km). Between 23 July and 9 August at Cape Vera, only $6.0 \pm 1.8\%$ of birds flying near the cliffs showed primary molt ($n = 7$ counts), whereas during this same period, $28.6 \pm 3.5\%$ of birds near the coast were in wing molt ($n = 18$; Mann–Whitney test, $U = 3.0$, $P < 0.001$; Fig. 1).

Primary molt scores

We detected considerable variability in PMS in our sample of birds known to contain non- or failed breeders from 2003 measured between 7 July and 18 August (PMS range 0–12). Of these birds, many non-zero PMS were obtained prior to hatch at the colony.

For birds in primary molt, we did not detect a difference between mean PMS for the left wing (3.7 ± 0.6, $n = 36$) and right wing (3.4 ± 0.6; paired $t_{35} = 1.24$, $P = 0.2$). Primary molt scores were perfectly symmetrical in 64% of the birds examined, and nearly symmetrical (PMS difference ≤ 1) in 80% of all individuals not identified as known breeders (Fig. 2). Only one individual exhibited a PMS difference >2 (PMS difference $= 6$).

We tested whether $\log_{10}$-transformed PMS in non- or failed breeding males differed from females, but there was a significant interaction effect of sex with date for both right and left wings ($F_{1,34} > 5.5$, $P < 0.03$). Instead, we compared PMS values between sexes in July and in August, using Mann–Whitney tests. We did not detect a significant difference in PMS between males and females for either month (all $P > 0.15$), except for a tendency for August males to
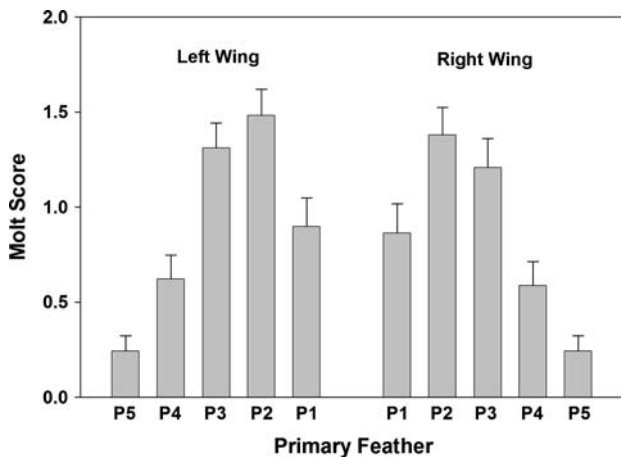
Fig. 2 Mean (SE) primary molt score of individual primary feathers using the Ashmole (1962) method, for the left and right wings of 29 northern fulmars exhibiting primary molt. Molt initiation was never observed for feathers P6–P10 in any birds at the colony

have lower PMS than females ($P = 0.082$), although samples sizes were small (Fig. 3). We could not test for a sex difference in PMS for our sample of individuals known to be breeders as none had initiated primary molt.

Molt of primary feathers was initiated at the second primary (P2), followed by P3, P1, P4 and P5 (Fig. 2), as indexed by the development scoring pattern from Ashmole (1962). No fulmars at the colony were observed molting feathers in the P6 to P10 positions. For 19 fulmars with molt in the secondary feather tracts, molt was initiated at an inner node, with 89% having blood quills in the S21 position, 68% in S20 and S19, 10% in S18, and 5% in S15. The maximum number of primary feathers being replaced per wing at a given time in any individual sampled was five
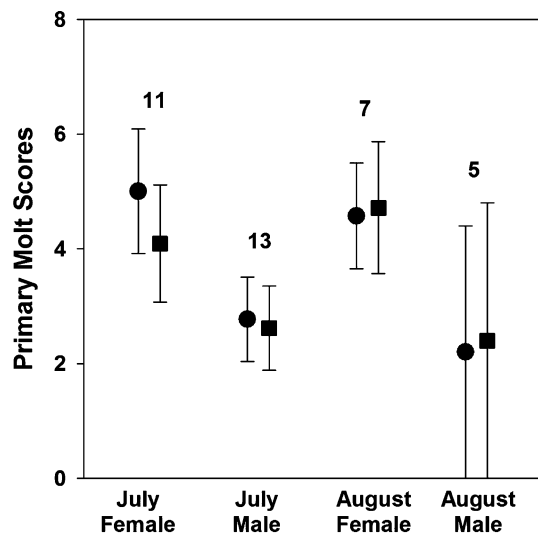
Fig. 3 Total primary molt scores for left (*circle*) and right (*square*) wings of failed and non-breeding fulmars

($n = 7$). Of these, no single feather obtained a molt score greater than three (i.e., vane more than two-thirds grown), which suggests that an even greater number of feathers undergoing replacement in an individual is possible.

Body molt

Although breeders showed no evidence of molt in flight feather regions in any year, molt onset was detected on other parts of the body in 13 of 64 adults (20%) captured at the nest. However, only those individuals captured near the end of the incubation period (four of five individuals captured within 2 weeks of hatch) exhibited mean molt intensity greater than 1% (mean 6.2%, range 2–11%). Among these individuals, molt had been initiated in the capital, side, collar, back, scapular, leg, and tail areas (Table 1).

Unlike active breeders, molt was initiated by non- or failed breeding fulmars in all feather regions examined in females, and all but the rectrices and flank feathers in males (Table 1). For these birds, molt had progressed most in the scapular and primary feather regions, as well as the head.

We did not detect a significant difference in the mean molt intensity between breeding male and female fulmars (Table 1; Mann–Whitney tests, all $P > 0.1$). However, female non- or failed breeding fulmars tended to have higher mean molt intensity in the crown ($P = 0.07$), cheek ($P = 0.06$), neck ($P = 0.04$) and wing covert ($P = 0.06$) feather regions than male non-breeders (Table 1). Overall, non-breeding females had a higher total molt score than non-breeding males ($P = 0.02$).

Discussion

Northern fulmars breeding in the Canadian High Arctic did not initiate primary feather molt during incubation or early chick-rearing, consistent with most observations from studies in the Boreal part of the fulmar's range (Wynne-Edwards 1939; Duffey 1950; Fisher 1952; Hatch and Nettleship 1998). However, failed or non-breeding birds were observed in primary molt as early as 23 June, approximately 2 weeks after the mean egg-laying date for the colony, as found elsewhere (Hatch and Nettleship 1998). Some breeding fulmars did initiate molt in other parts of their body, notably the neck, upper back, and flank regions. Nonetheless, total molt scores for breeding and non-breeding birds indicated no molt to light molt (Thompson and Drobney 1995). Molt may be energetically-expensive in petrels; Chu (1984) found that shearwaters lost 12% body mass during molt. Thus, in the High Arctic, fulmars appear to temporally segregate primary molt and reproduction.

Our results confirm the unusual molt pattern suggested by Thompson et al. (2000), whereby fulmars, sooty shear-

waters (*Puffinus griseus*) and certain albatrosses (Tickell 2000) initiate primary molt at P2. In fulmars, the progression was rapid, with P2–P3 and then P1 and P4 almost molting as a block. This pattern is different from most other seabirds, notably the other procellariids, where the typical primary molt sequence initiates at P1. Also consistent with Thompson et al. (2000), we found that secondary molt was initiated at an inner node, with considerable changeover of S18–21. However, none of the fulmars we examined had initiated secondary molt at a second node, despite being in the process of replacing up to four of the innermost secondaries. Thompson et al. (2000, p. 50) stated that "shortly after molt begins at the inner node, secondary molt begins at a middle node (S5)...". The rate of feather replacement may differ between High Arctic and Boreal fulmar populations, but at present we lack data to evaluate this possibility.

The timing of primary molt clearly differs among northern fulmar colonies, which is probably related to differences in nesting dates (Mallory and Forbes 2007). Fulmars nesting in different parts of the British Isles may exhibit large differences in molt chronology (Ginn and Melville 1983). On 10 July 1960, Bourne (1966) observed 33% of the fulmars at St. Kilda, UK in primary molt, while around this date only 6% of fulmars at Cape Vera were in primary molt (Fig. 1). However, mean egg-laying dates at these colonies differ by approximately 1 month (Mallory and Forbes 2007). Thus, at the same stage of the breeding season, about 26% of fulmars at Cape Vera were exhibiting primary molt (Fig. 1). In contrast, Hatch (1979) found a peak of approximately 75% of fulmars at the Semidi Islands, Alaska colony exhibiting primary molt in mid-July in 1977, and the first week of August in 1976. Moreover, the earliest birds in primary molt were seen 24 May. The highest proportion of molters observed at Cape Vera was 57% on 11 August, with primary molt first observed on 23 June. Typical mean egg-laying and hatch dates differed by only 2 days between Hatch's Alaskan site and Cape Vera, yet primary molt initiation and peak proportional occurrence were observed 1–4 weeks earlier in Alaska. We speculate that either colony attendance dynamics of non-breeders (outlined below), or the timing of molt in relation to mean egg-laying dates or migratory habits (Bridge 2006) differ for fulmars in the North Pacific and North Atlantic populations.

Harris (1971) and Verbeek (1977) have hypothesized that differences in food availability and/or changes in foraging strategies during some years might explain differences in molt initiation dates between populations and years. For most bird species, reproduction occurs in synchrony with maximum food availability, due to high energetic costs to breeding adults. Hence, reproduction and molt may only be temporally exclusive in situations where food resources are limited or when specific ecological constraints otherwise determine allocation of energy budgets. In years with abundant food, parent birds might be able to both feed young and initiate molt earlier than expected. If this is the case, changes in patterns of molt chronology, both within and between populations over time, might serve as indicators of ecological conditions in the marine environment.

Furthermore, timing of molt may be related to environmental conditions or energetic requirements that are specific to given populations or locations. For example, local availability of, and access to, natural or anthropogenic food resources (Harris 1971), geographic constraints (i.e., migration duration and distance; Holmgren and Hedenström 1995), photoperiod (Lesher and Kendeigh 1941; Lindstrom et al. 1994), and ice conditions could lead to regionally-specific molt timing. Environmental conditions that vary widely within the fulmar's distribution range might explain the variability in molt chronologies among colonies reported in the literature.

Hatch (1979, 1989) surmised that seasonal and annual patterns of fulmar colony attendance, including the timing of molt, were linked to annual marine productivity. If we assume that the relative timing of nest failure was similar between these colonies, then we propose two possible explanations for the difference in the timing of molt compared to breeding in Alaska and Cape Vera. First, proportionally more non-breeding birds exhibiting wing molt may attend Alaskan colonies relatively earlier in the breeding season, compared to High Arctic fulmars. This may be possible, but Hatch (1989) speculated that many non-breeding birds arrived at the Alaskan colonies in August. Second, non-breeding High Arctic fulmars may delay entering wing molt until later in the season when local marine productivity is higher (Raymont 1976). Although we lack data to test these two hypotheses, we note that low marine productivity early in the breeding season probably accounts for the relatively long pre-laying exodus (Mallory and Forbes 2007) and incubation shifts (Falk and Møller 1995; Gaston et al. 2005) in High Arctic fulmars.

A difference in the proportion of birds showing signs of molt between those observed near nesting ledges and those observed farther away from the colony, suggests that individuals visiting the colony, probably breeders and recently failed breeders, were slower to initiate wing molt than other conspecifics (see Fig. 1). It therefore is likely that, in addition to known breeders, a significant proportion of the sampled birds shot along the shoreline near the colony consisted of failed breeders and non-breeding juveniles. This finding is in agreement with results of telemetry studies conducted at the site, where breeding birds all left the colony to feed hundreds of kilometres to the east (Mallory, unpublished data), and also was confirmed in part through internal examination of carcasses. Also, this result highlights the importance of colony-specific information for use in intercolony comparisons. We cannot rule out the possi-

bility that some of the variation in molt proportions observed among fulmar colonies could be related to differences in local, unreported movements of breeding, non-breeding and failed breeders.

We found that non- or failed breeding female fulmars were somewhat more advanced in molt than non- or failed breeding males, but there was little progression of molt between July and August in non-breeders. This observation is probably attributable to more advanced, non-breeding molters leaving the colony for pelagic zones to molt their outer primaries (Brown 1988) while new molters (recently failed breeders) enter the near-colony molting group, resulting in little apparent change in molt progress. Also, the overall percentage of molt intensity was low in both sexes (Table 1). We suspect that this pattern is driven by failed breeders, and may be attributable to the timing of contributions to incubation by each sex. For example, a female may lay its egg and then find itself in relatively poor physical condition, and abandon the nesting attempt (and thus, could potentially shift resources towards molt). Because its partner takes the first incubation shift for up to 2 weeks, the male may not realize that the attempt has been abandoned until the female fails to return. Similarly, if a female returns to find that the nest has been lost during the male's first shift, it would be in relatively good condition, and could immediately switch resource allocation towards molt. In contrast, the male may first have to recover resources lost during the incubation shift before being in suitable condition to initiate molt.

The factors that determine molt progress in fulmars remain to be explored fully. Despite advances in knowledge of fulmar reproduction, diet, and body condition, we consider that the potential for molt chronology to serve as an ecological metric remains presently dubious, in the absence of studies at other sites. Nonetheless, our study documented consistent patterns over 3 years at one High Arctic site, and similar patterns at a second site. These should serve as a suitable baseline set against which future comparisons can be made. Documenting this baseline is timely, as ecological conditions are changing in the Arctic, and fulmars are known to respond to these environmental changes (Thompson and Ollason 2001; Gaston et al. 2005). Given the ease with which primary molt can be observed and recorded, we suggest that investigation of ecological factors affecting timing and duration of molt in many seabird species could lead to the use of molt, especially primary molt, as a possible indicator of ecological change. We suggest that all studies at fulmar colonies include regular (at least weekly), standardized surveys of molting birds within the core colony to detect date of first primary molt, and the proportion of molting birds in relation to date of egg-laying and hatching. Such quantitative studies of molt timing and rate in relation to sex, age, breeding success, and foraging consid-

erations, among different populations and using common methodologies, are clearly warranted for this and other broadly-distributed species.

References

Ashmole NP (1962) The black noddy (*Anous tenuirostris*) on Ascension Island. Ibis 103:235–273

Barbraud C, Chastel O (1998) Southern fulmars molt their primary feathers while incubating. Condor 100:563–566

Beck JR (1970) Breeding seasons and moult in some smaller Antarctic petrels. In: Holdgate MW (ed) Antarctic ecology, vol 1. Academic Press, London

Bridge ES (2006) Influences of morphology and behavior on wing-molt strategies in seabirds. Marine Ornithol 34:7–19

Bourne WRP (1966) The plumage of the fulmars of St. Kilda in July. Bird Study 13:209–213

Brown RGB (1988) The wing-moult of fulmars and shearwaters (Procellariidae) in Canadian arctic waters. Can Field Nat 102:203–208

Carrick R, Dunnet GM (1954) Breeding of the fulmar *Fulmaris glacialis*. Ibis 96:356–370

Chu EW (1984) Sooty shearwaters off California: diet and energy gain. In: Nettleship DN, Sanger GA, Springer PF (eds) Marine birds: their feeding ecology and commercial fisheries relationships. Can Wildl Serv Spec Publ, Ottawa, pp 64–71

Dott HEM (1973) Fulmars at land in summer and autumn. Bird Study 22:255–259

Duffey E (1950) Non-breeding in the fulmar *Fulmarus glacialis*. Scott Nat 62:111–121

Edwards DB, Mallory ML, Forbes MR (2005) Variation in baseline haematology of northern fulmars (*Fulmarus glacialis*) in the Canadian high arctic. Comp Clin Path 14:206–209

Falk K, Møller S (1995) Breeding ecology of the fulmar *Fulmarus glacialis* and the kittiwake *Rissa tridactyla* in high-arctic northeastern Greenland, 1993. Ibis 139:270–281

Fisher J (1952) The fulmar. Collins Publishing, London

Frederiksen M, Harris MP, Daunt F, Rothery P, Wanless S (2004) Scale-dependent climate signals drive breeding phenology of three seabird species. Glob Change Biol 10:1214–1221

Gaston AJ, Gilchrist HG, Mallory ML (2005) Variation in ice conditions has strong effects on the breeding of marine birds at Prince Leopold Island, Nunavut. Ecography 28:331–344

Ginn HB, Melville DS (1983) Moult in birds. Tring: British Trust for Ornithology

Grosbois V, Thompson PM (2005) North Atlantic climate variation influences survival in adult fulmars. Oikos 109:273–290

Hamer KC, Schreiber EA, Burger J (2002) Breeding biology, life histories, and life history–environment interactions in seabirds. In: Schreiber EA, Burger J (eds) Biology of marine birds. CRC Press, New York, pp 217–261

Harris MP (1971) Ecological adaptations of moult in some British gulls. Bird Study 18:113–118

Hatch SA (1979) Breeding and population ecology of northern fulmars (*Fulmarus glacialis*) at Semidi Islands, Alaska. MSc Thesis, University of Fairbanks, Alaska

Hatch SA (1989) Diurnal and seasonal patterns of colony attendance in the northern fulmar, *Fulmarus glacialis*, in Alaska. Can Field Nat 103:248–260

Hatch SA, Nettleship DN (1998) Northern fulmar (*Fulmarus glacialis*). In: Poole A, Gill F (eds) The Birds of North America, no. 361. The Birds of North America, Philadelphia

Hodum PJ, Hobson KA (2000) Trophic relationships among Antarctic fulmarine petrels: insights into dietary overlap and chick provisioning strategies inferred from stable-isotope (δ^{15}N and δ^{13}C) analyses. Mar Ecol Prog Ser 198:273–281

Holmgren N, Hedenström A (1995) The scheduling of molt in migratory birds. Evol Ecol 9:354–368

Hunter S (1984) Moult of the giant petrels *Macronectes halli* and *M. giganteus* at South Georgia. Ibis 126:119–132

King JR, Murphy ME (1985) Periods of nutritional stress in the annual cycles of endotherms: fact or fiction? Am Zool 25:955–964

Lesher SW, Kendeigh SC (1941) Effect of photoperiod on molting of feathers. Wilson Bull 53:169–180

Lindström A, Daan S, Visser GH (1994) The conflict between moult and migratory fat deposition: a photoperiodic experiment with bluethroats. Anim Behav 48:1173–1181

Mallory ML, Fontaine AJ (2004) Key marine habitat sites for migratory birds in Nunavut and the Northwest Territories. Can Wildl Serv Occas Pap No 109

Mallory ML, Forbes MR (2005) Sex discrimination and measurement bias in northern fulmars (*Fulmarus glacialis*) from the Canadian arctic. Ardea 93:25–36

Mallory ML, Forbes MR (2007) Does sea-ice cover constrain the breeding schedules of high arctic northern fulmars? Condor (in press)

Mallory ML, Braune BM, Forbes MR (2006a) Breeding and contaminant concentrations in northern fulmars (*Fulmarus glacialis* L.) from the Canadian high arctic. Chemosphere 64:1541–1544

Mallory ML, Forbes MR, Galloway TD (2006b) Ectoparasites of northern fulmars *Fulmarus glacialis* (Procellariiformes: Procellariidae) from the Canadian Arctic. Polar Biol 29:353–357

Norstrom RJ, Clark TP, Kearney JP, Gilman AP (1986) Herring gull energy requirements and body constituents in the Great Lakes. Ardea 74:1–23

Payne RB (1972) Mechanism and control of molt. In: Farner DS, King JR (eds) Avian biology, vol 11. Academic Press, New York

Petrie SA (1998) Intensity and chronology of breeding and post-breeding moult in White-faced Whisting-Ducks (*Dendrocygna viduata*). Wildfowl 49:207–218

Raymont JEG (1976) Plankton and productivity in the oceans. Pergamon Press, Toronto

Ricklefs RE (1974) Energetics of reproduction in birds. In: Paynter RA (ed) Avian energetics. Publ Nuttall Ornithol Club 15

Robertson GJ, Cooke F, Goudie IR (1998) Moult speed predicts pairing success in male harlequin ducks. Anim Behav 55:1677–1684

Salomonsen F (1965) The geographical variation of the fulmar (*Fulmarus glacialis*) and the zones of marine environment in the North Atlantic. Auk 82:327–355

Swaddle JP, Witter MS (1997) The effects of molt on the flight performance, body mass, and behavior of European starlings (*Sturnus vulgaris*): an experimental approach. Can J Zool 75:1135–1146

Systat Software Inc (2002) Systat 10.2. Systat, Richmond

Thompson CW, Hatch SA, Leu M, Brennan K, Roca B, Krausse B (2000) Novel sequences of flight feather molt in sooty shearwaters and northern fulmars. Pac Seabirds 27:50

Thompson DR, Furness RW (1995) Stable-isotope ratios of carbon and nitrogen in feathers indicate seasonal dietary shifts in northern fulmars. Auk 112:493–498

Thompson JE, Drobney RD (1995) Intensity and chronology of post reproductive molts in male canvasbacks. Wilson Bull 107:338-358

Thompson P, Ollason JC (2001) Lagged effects of ocean climate change on fulmar population dynamics. Nature 413:417–420

Tickell WLN (2000) Albatrosses. Yale University Press, New Haven

Titman RD, Lagrenade MC, Miller MR (1990) An evaluation of techniques to measure contour feather molt in ducks. J Wildl Manage 54:219-222

Verbeek NAM (1977) Timing of primary moult in adult herring gulls and lesser black-backed gulls. J Ornithol 118:87–92

Visser ME, van Noordwijk AJ, Tinbergen JM, Lessells CM (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). Proc R Soc Lond Ser B 265:1867–1870

Warham J (1996) The behaviour, population biology and physiology of the petrels. Academic, London

Weimerskirch H (1991) Sex-specific differences in molt strategy in relation to breeding in the Wandering Albatross. Condor 93:731–737

Wynne-Edwards VC (1939) Intermittent breeding of the fulmar (*Fulmarus glacialis*), with some general observations on non-breeding in sea-birds. Proc Zool Soc Lond Ser A 109:127–132