

THE MOLT CYCLE OF THE ARCTIC TERN, WITH COMMENTS ON AGING CRITERIA

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Abstract.—Molt-data from museum specimens of Arctic Terns (*Sterna paradisaea*) were analyzed and considered in relation to other life-history aspects. Differences in shape and color of outer tail feathers were reliable indicators of age class, allowing second-year birds to be distinguished from third-year birds, and second- and third-year birds from after-third-year birds. No differences in molt pattern were found between subadult age classes, or between subadult and adult age classes. The duration of primary molt was estimated at 99 d for adults and 221 d for subadults. This difference in time allotted to molt probably results from constraints imposed on adults by migration and breeding. Adults replace all their flight feathers on the wintering grounds, whereas subadults often complete this molt in tropical latitudes where they summer. Arctic Terns appear to exhibit the second inner primary molt featured by most other *Sterna* species.

EL CICLO DE MUDA DE *STERNA PARADISAEA* Y COMENTARIOS SOBRE LOS CRITERIOS PARA ASIGNAR EDADES

Sinopsis.—Se analizaron los datos de muda de especímenes de museo de *Sterna paradisaea* y se consideraron en relación a otros aspectos de su historia natural. Las diferencias en la forma y el color de las rectrices externas fueron indicadores confiables de las edades, permitiendo que aves del segundo año se puedan distinguir de aves del tercer año, y que aves del segundo y tercer año se puedan distinguir de aves mayores de tres años. No se hallaron diferencias en los patrones de muda entre las clases de aves subadultas, o entre las clases de edad adultos y subadultos. La duración de la muda primaria se estimó en 99 días para los adultos y de 221 días para los subadultos. Esta diferencia en tiempo asignado a la muda probablemente resulta de limitaciones impuestas en los adultos por la migración y la reproducción. Los adultos rempazan todas sus plumas de vuelo en las localidades invernales, mientras que los subadultos a menudo completan esta muda en latitudes tropicales donde pasan el verano. *Sterna paradisaea* parece exhibir la muda de la segunda primaria interna característica de la mayoría de las otras especies de *Sterna*.

The yearly energy budgets of birds are taxed by three major costs: molting, breeding, and migrating. Although a major energetic demand in the annual cycle (Murphy and King 1992, Murphy and Taruscio 1995, Taruscio and Murphy 1995, Walsberg 1983), molt has been little studied. This is true despite the fact that museum specimens constitute a huge and readily available data set for the study of molt (Rohwer and Manning 1990). Given the metabolic, thermoregulatory, and flight costs of molt, quantitative knowledge of molt cycles of individual species, rather than reliance on sweeping generalities of patterns among groups, is critical to understanding the life-history strategies of birds. A case in point is the Arctic Tern (*Sterna paradisaea*). The only quantitative data available on the molt cycle of adults is a description of feather condition in 15 specimens, just five of which were actively growing primaries (Stresemann and Stresemann 1966). This lack of data has led to conflicting speculations as

to when and how long Arctic Terns molt, as well as to conflicting ideas over which feather tracts are involved in each molt and how often feather tracts are replaced (Cramp 1985, Ginn and Melville 1983, Stresemann and Stresemann 1966, Watson 1975). Furthermore, based on this limited data set, it was assumed that this species did not exhibit the second replacement of inner primaries (b' series of Stresemann and Stresemann 1966) characteristic of most other *Sterna* species.

This study was undertaken to attempt to clarify and resolve these issues. I present data that show that Arctic Terns appear to possess a second inner primary molt; they also replace at least some crown feathers twice in one nonbreeding season, a pattern similar to other species in the genus, but a pattern which seems to have been misinterpreted. Both of these molt features may have important life-history functions beyond the simple need to replace worn feathers (Voelker 1996). In this paper, I seek to (1) define reliable age characters for placing Arctic Terns in year classes and (2) describe the molts of the Arctic Tern.

MATERIALS AND METHODS

This study is based on 338 Arctic Tern specimens: 230 adult specimens and 108 sub-adult specimens. Of these, 56 adult and 25 subadult specimens were replacing flight feathers. Specimens were assembled from (1) major museums from throughout the world, (2) museums in countries with a history of Antarctic Research, and (3) larger museums in countries within the range of the Arctic Tern (for museums and museum abbreviations, see Acknowledgments).

Scoring molt.—Arctic Terns have 11 primaries and 18 secondaries (Ginn and Melville 1983) per wing, and 12 rectrices. Primaries were numbered P1–P10, P1 being most proximal (closest) to the body. The eleventh primary is vestigial (Stresemann 1963, Stresemann and Stephan 1968), and I did not include it in this study. Secondaries were numbered S1–S18, S18 being most proximal to the body. Rectrices were numbered R1 (innermost) to R6 (outermost) on each side. I determined the presence of molting flight feathers by lifting covert feathers with forceps and a dissecting probe. A molt score was assigned to each flight feather (remiges and rectrices) as follows: (0) old; (1) missing or in pin; (2) opened pin to one-third grown; (3) one-third to two-thirds grown; (4) two-thirds to full-grown, with sheathing; (5) full-grown, with no sheathing (Ashmole 1962, 1963, Ginn and Melville 1983). Possible scores range from zero (all old feathers) to 340 (all new feathers). I considered missing or partially grown feathers to be molting only if molt was occurring, or had recently been finished, in the corresponding tracts on both sides of the body. Because birds tend to begin molt with primary feathers, I considered growing tail feathers that preceded initiation of primary molt to have been lost adventitiously unless replacement was symmetrical. I also examined the head and body of each specimen for molt, using a dissecting probe to lift feathers so I could examine feather bases and tracts, assigning a plus (molting) or minus (not molting) to the following regions:

head, upperbody, and underbody. Molt terminology follows that of Humphrey and Parkes (1959). I estimated the rate and duration of molt using Pimm's (1976) regression method employing date as the dependent variable and molt score as the independent variable, which provides an estimate of molt duration for individuals. For the regression analysis, collection dates were converted to Julian dates (e.g., 1 Jan. = JD 1, 31 Dec. = JD 365). Because this species molts across two calendar years, I made Julian dates additive in the second year.

Few specimens were collected away from the breeding range. To add birds from as many different dates as possible I included seven molt scores that are based either on birds I did not examine, or on birds with uncertain collection dates. I examined one (AMNH 448054) of the six specimens collected by the British, Australian, and New Zealand Expedition; the other five are unaccounted for (B. Gill, pers. comm.). Falla (1937) gave a description of the stage of molt for all six of these specimens, and based on my examination of AMNH 448054 and the descriptions given by Falla, I have given a molt score to the five missing specimens. Because body, primary, and rectrix condition were accurately described for the specimen I examined, I scored these feathers on the unseen specimens according to the given descriptions. Secondaries were not described, but because AMNH 448054 had almost completed secondary molt, and because most molting specimens in the study had finished growing secondaries before primaries, I assumed that the secondaries for the other five subsequently collected specimens were new and fully grown.

Friedmann (1945) described the body and primaries of a specimen collected by H. M. Bryant on 25 Feb. 1940; I assumed completed growth of both the secondaries and rectrices.

The seventh score requiring explanation was assigned to AM 22090, a specimen with no collection date and of dubious collection locality, known to have been collected by Mawson's Expeditions to Antarctica, 1911–1914. I examined both the specimen and Mawson's (1915) accounts of his expeditions, and found that he noted the collection of Arctic Terns on two occasions, the first being on Macquarie Island. As the collection occurred on 6 Aug. 1913 and the bird is heavily molting, I have ruled out Macquarie Island as the collecting site. The other bird was collected on 16 Jan. 1914, a date that, by comparison to the molt stage of other Antarctic specimens observed in January (Zink 1981a) would fit this specimen. The exact collection locality is not listed, but on 17 January the position of the expedition was 62°21'S, 95°9'E. I have used this as its collection locality.

Molt and migration.—Because the Arctic Tern has a circumpolar breeding distribution (Cramp 1985, Harrison 1983), I consider any specimen collected at greater than 50° North latitude to be on the breeding grounds ($n = 142$). Because most Arctic Terns are generally associated with pack ice on their wintering grounds (Cline et al. 1969, Erickson et al. 1972, Zink 1981b, but see Morant et al. 1983), and the limit of pack ice varies around Antarctica between 50° and 60° (Espenshade 1991), I

treated birds from greater than 50° South latitude as being on their wintering grounds ($n = 81$). Migratory range includes any specimen collected between 50° South and 50° North latitude ($n = 115$).

Age identification.—Subsequent to losing juvenal plumage, Arctic Terns in basic plumage are difficult to assign to age class (Cramp 1985). Because the majority of individuals begin breeding in their fourth or fifth year (Bianki 1977, Coulson and Horobin 1976, Cramp 1985, Horobin 1969), I sorted all specimens into the following age classes (from Pyle et al. 1987): hatching year (HY), birds in their first calendar year; second year (SY), birds in their second calendar year; third year (TY), birds in their third calendar year; and finally, after third year (ATY), any bird in at least their fourth calendar year. Hatching year, sub-adult (SY and TY), and ATY plumages are generally well described (Cramp 1985, Fjeldså 1977, Harrison 1983). Identification of HY birds and ATY birds is simple due to “scaling” on most feathers of HY birds and lengthy outer rectrices of ATY birds. Adults in the process of replacing the characteristic outer rectrices can be confused with sub-adult birds, but they may still be identified as adults by their lack of a carpal bar (Harrison 1983).

Distinguishing SY and TY birds is difficult. These two year classes closely resemble each other year-round. To find plumage characters that would distinguish these two age classes, I sorted all birds by month, identified HY and ATY birds, then evaluated several different characters that others had suggested were useful in identifying sub-adult age classes. Carpal bar (Harrison 1983) and plumage and soft part coloration (Hawksley 1950, Palmer 1941) all were unreliable, but I did find a reliable difference in rectrix coloration and shape that distinguishes SY and TY birds. Additionally, I measured the length of the sixth rectrix and difference between the lengths of the fifth and sixth rectrices for SY, TY, and ATY birds to determine if tail morphometrics are useful in discriminating between age classes. I performed one-way ANOVA and Tukey HSD Pairwise Post-hoc Comparisons (Wilkinson 1989) on these measurements. I used multiple regression (analysis of covariance with interaction; Wilkinson 1989) to determine if differences in molt duration existed between these two age classes.

RESULTS

Distinguishing second-year from third-year birds.—The shape and color of the outermost rectrices proved to be a reliable indicator of age class for these specimens. During their first flight feather molt (end of HY/beginning of SY) birds lose their sixth rectrices which are short, with either both vanes mostly white (this study) or with the outer vane gray and the inner vane white (Cramp 1985), and replace them with gray feathers; these rectrices are carried during most of the SY. Both vanes of these new feathers were dark gray and generally tipped with a white spot. The feathers are also shaped differently than those found after later flight feather molts: after the first flight feather molt, sixth rectrices are wedge shaped, after subsequent flight feather molts, sixth rectrices are narrowly tapered.

TABLE 1. Between age-class comparison of tail length and difference between fifth and sixth rectrices. Measurements are in millimeters.

Age (<i>n</i>)	Tail length		Difference between rectrices 5 and 6	
	\bar{x}	SD	\bar{x}	SD
SY (10)	136.1	7.1	32.4	6.8
TY (3)	139.6	5.4	33.8	3.6
ATY (9)	171.2	5.6	54.0	5.3

Two specimens (USNM 394707, 394708) prove that the distinctive gray rectrices are acquired after the first flight feather molt. Both still retain several juvenal body feathers (i.e., "scaled"), but have acquired the outer rectrix shape and coloration that is carried during the second year. After the second flight feather molt (end of SY/beginning of TY) birds possess sixth rectrices more adult-like in both coloration and feather shape (little gray and tapered).

The length of the sixth rectrix and the difference in lengths of the fifth and sixth rectrices do not significantly differ between SY and TY birds for either character ($P = 0.68$ and 0.93 , respectively). However, both characters are significantly greater in ATY than in either SY or TY birds ($P < 0.001$; Table 1).

I found other potential plumage characters used to define age class in Arctic Terns to be either ambiguous, impossible to assess on museum specimens, or missing from most specimen tags. I found the use of carpal bar color (Harrison 1983) and body coloration (Hawksley 1950, Palmer 1941) too variable across SY and TY birds. I was unable, using either criterion, to place individual SY and TY birds from a given month consistently into the same age category. While perhaps useful in the field, specimen soft part colors are typically useless due to fading, and unfortunately these data are infrequently recorded on specimen tags.

Naming molts.—To maintain a homologous nomenclature across *Sterna*, I have named the body molts of Arctic Terns in keeping with other published accounts of molts in *Sterna* (Cramp 1985, Wilds 1993). However, the flight feather molt of the Arctic Tern does not lend itself to being easily homologized with the flight feather molts of other *Sterna*. Some *Sterna* species breeding in the northern hemisphere initiate a second primary molt after, or simultaneously with, the completion of the initial replacement of all primaries (Stresemann and Stresemann 1966). Although the Arctic Tern also exhibits this pattern (see below), the timing of the molts compared to other species (see Cramp 1985) is not homologous. Still other *Sterna* species do not exhibit this pattern of primary replacement. Maintaining homologies is difficult, and therefore flight feather data are presented separately from prebasic and prealternate body molt data.

Prebasic body molts.—I found only two HY birds that were replacing

some body feathers, both collected in November, and speculate that they are beginning first prebasic body molt. Although this requires verification if and when more material become available, Arctic Terns as well as other tern species have been observed replacing juvenal body plumage (i.e., in first prebasic molt) as early as October (Cramp 1985, Wilds 1993). Identification of this molt as the first prebasic body molt allows me to maintain homologies for later molts. The first prebasic body molt should be a complete body molt which causes a conspicuous change in appearance by replacing the "scaled" juvenal plumage with subadult plumage.

I found six SY specimens undergoing second prebasic body molt, and two TY specimens undergoing third prebasic body molt. Molt occurs on the head, upperparts, and underparts, and imparts no overall change in aspect. Of these eight birds, four were collected on the breeding grounds and four within the migratory range, all between July and September.

The definitive prebasic body molt has historically been deemed a complete molt of the head, upperparts, and underparts (Cramp 1985). In the resulting plumage, ATY birds supposedly displayed a white crown and underparts, fresh gray upperparts, and perhaps some new rectrices. I found no evidence to support this. I examined no adult specimens with a completely white crown, or with completely white underparts. Instead, this molt serves primarily to "mottle" the crown and, to a lesser extent, suffuse the underparts with a varying number of white feathers. The crown remains predominantly black, the body predominantly gray. The most noticeable difference between definitive basic and definitive alternate crown plumages is coloration: definitive basic crown plumage includes a scattering of white feathers in an otherwise black crown that is strikingly different from the solid black crown of the definitive alternate crown plumage. I found no black feathers being grown in the crown during this molt.

The definitive prebasic body molt occurs between June and November, predominantly on the breeding grounds. Of the 31 specimens collected during southward migration, 68% had completed definitive prebasic body molt, 13% were actively molting, and 19% had not yet initiated molt.

Prealternate body molts.—All head, upperbody, and underbody feathers are replaced during these molts. First and second prealternate body molts occur in conjunction with the first and second flight feather molts, respectively (Table 2); there is no significant overall change in body plumage appearance. Given that SY and TY birds have no fixed movement pattern (Morant et al. 1983), these molts can begin on the wintering grounds or in the migratory range, and be completed in either of these regions as well.

Definitive prealternate molt is a complete molt of the head, upperbody, and underbody, that results in the black cap and gray upper- and underparts of breeding birds. This molt occurs in conjunction with the definitive flight feather molt (Table 2) on the wintering grounds.

Flight feather molts.—Arctic Terns initiate flight feather molt for the first time in their life while still in their HY and complete this molt early in

TABLE 2. Number of SY, TY, and ATY specimens molting various feathers by month. Numbers in parentheses in rows denoting flight feather molt indicate that only rectrix molt is occurring, dashes indicate no specimens in that category.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Body + flight feathers	SY	2	0	0	0	—	(5)	—	—	0	—	—	—
	TY	1	4	1 + (1)	2		(6)			(1)			
	ATY	6	42	2 + (6)	0		0			(2)			
Flight feathers only	SY	—	1	0	—	—	0	—	0	—	—	—	—
	TY		0	1			1		(1)				
	ATY		0	0			0		0				
Body only	SY	—	—	0	—	—	—	2	2	2	0	—	—
	TY			0				1	0	0	0		
	ATY			1				2	11	10	4		
None	SY	1	—	0	0	1	4	4	2	1	7	9	1
	TY	0		0	0	1	0	0	0	0	1	1	0
	ATY	0		1	4	20	47	37	21	1	2	2	0
No molt, but mottled crown	ATY	—	—	—	—	—	—	—	—	1	3	6	1

their SY. Their second flight feather molt is initiated at the end of their SY and completed in the beginning of their TY. Definitive flight feather molt occurs in birds completing their TY and beginning their fourth year (ATY), and in all subsequent calendar year boundaries. All ATY specimens in flight feather molt were collected on the wintering grounds, as were all subadults which were replacing primaries. Eleven subadults collected in the migratory range were still replacing rectrices.

I was unable, given the low sample sizes of molting subadults available, to detect any differences between the sequence or extent of primary replacement in first, second, and definitive flight feather molts, and so present these data together. Primaries are replaced distally from at least P6 to P10, as evidenced by the fact that in all but four cases (which indicate a special molt pattern, and are discussed elsewhere) any given proximal feather is always further along in the molt replacement process than is the next most distal feather. I found no specimens molting P1–P5, so neither the direction of replacement (distally or proximally), nor whether P1–P5 form part of the same molt series as P6–P10 can be inferred. However, P1–P5 were in all instances new feathers on specimens molting P6–P10, and limited data on other *Sterna* species indicated that primaries are replaced from P1–P10 (Stresemann and Stresemann 1966). However, in several species of albatross, P1–P5 and P6–P10 molt according to different rules, and in different directions (Langston and Rohwer 1995).

One subadult Arctic Tern specimen (NMCAN 60245) has P2–P8 = 5, P9 = 4, P10 = 3, and, surprisingly, P1 = 1. Since P2–P8 are new, this specimen along with three adult specimens exhibiting the same pattern (NMCAN 60244, 60246, USNM 536538), shows that at least some Arctic

TABLE 3. Relationships among secondary feathers for all specimens actively replacing secondaries (left wing only; S18 = closest to body).

	Secondary number																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Next most proximal longer/More fully grown	0	0	0	0	0	0	0	0	0	0	0	2	30	10	3	0	0	—
Next most distal longer/More fully grown	—	1	2	3	4	4	6	9	14	22	26	2	0	0	0	0	0	0
Both adjacent longer/More fully grown	—	0	0	0	0	0	0	0	0	0	1	36	0	0	0	0	0	—

Terns exhibit the second inner primary molt (SIPM) displayed by many other species of *Sterna* (Cramp 1985, Stresemann and Stresemann 1966 and references therein). That a SIPM in Arctic Terns has gone unnoticed is because it overlaps in time with the molt of the outermost primaries and, thus, does not result in inner primaries appearing fresher than outer primaries.

One subadult specimen (BM[NH] 44.1.1829) from the wintering range was in flight feather molt, but not body molt, had nearly completed secondary molt, and just begun rectrix molt. This bird has delayed primary molt to such an extent that P1–P7 are growing simultaneously, and are all approximately the same length (all category 2); P8–P10 have yet to be dropped. This condition has been documented on several occasions (Parmelee 1977).

Secondaries are replaced bidirectionally. S11 is part of an outer secondary series (S1–S11) that is replaced proximally; S12 is part of an inner series (S14–S12) that is replaced distally (Table 3). Although data from Table 3 suggest that S15 is part of the S14–S12 series, an open-wing diagram in Bierman and Voous (1950) indicates that it is likely the first feather to be replaced in a proximally replaced series S15–S18. S12 is most often the last secondary to be replaced as evidenced by specimens having feathers adjacent to S12 more fully grown. Therefore, the inner series of secondaries typically finishes replacing feathers last, with one exception where S11 was still growing and S12 was more fully grown (Table 3). I have no specimens to verify the direction of replacement of some secondaries (S16–S18; but see Bierman and Voous 1950).

The sequence of rectrix replacement varies among individuals. In cases where I could infer which rectrix would have been the last to reach full growth R6 was typically the last to complete growth ($n = 40$) and R5 next most frequent ($n = 18$). Occasionally R2 ($n = 6$) or R1 ($n = 3$) would have been last. Although subadult rectrices are often being replaced in June, along with some body molt (Table 2), they are not part of a second limited tail molt as has been inferred (Cramp 1985, Ginn and Melville 1983), because there are no apparent wear differences as would be expected if they were replaced later. Adults are also frequently still molting

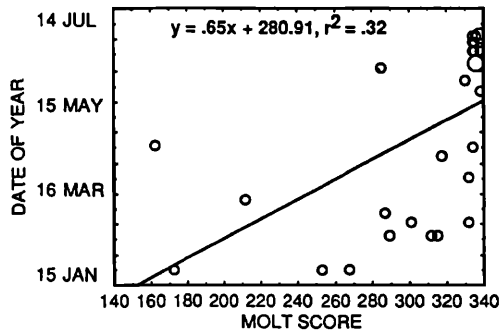


FIGURE 1. Regression estimating duration of first and second flight feather molts.

rectrices and body feathers after completing the primary and secondary series (Table 2). This is clearly a completion of the flight feather molt and prealternate body molt, rather than a distinct, limited molt of the tail and body feathers.

In order to derive some estimate of molt duration, I made two assumptions about primary replacement in Arctic Terns. I assumed that P1–P5 are replaced distally from P1 and that P1–P10 form a single series and are molted successively from P1. This is consistent with other *Sterna*.

Multiple regression indicated molt score to be a significant predictor of date ($F_{1,26} = 12.02$, $P = .0018$) for birds in first and second flight feather molt, but the difference between these age classes is not significant ($F_{2,24} = 1.13$, $P > 0.05$). The regression estimate gives average flight feather molt initiation date for SY and TY birds as 8 October, and the average completion date as 17 May, with a duration of 221 days (Fig. 1). The regression estimate for ATY birds gave an average initiation date of 20 November, and average completion date of 27 February (99 days; Fig. 2).

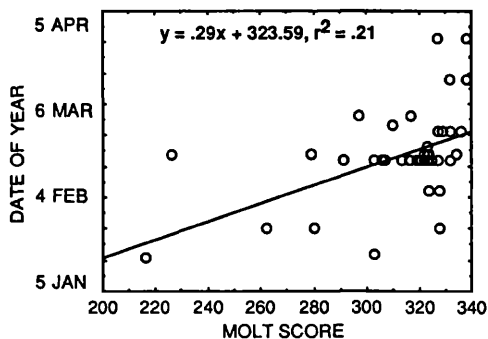


FIGURE 2. Regression estimating duration of definitive flight feather molt.

DISCUSSION

Although I examined 20 HY specimens collected either on the breeding grounds or within the migratory range, none of these specimens had as yet begun the first flight feather molt. Based on the initiation dates derived from the regression (Fig. 1), at least some of these birds could have been expected to be exhibiting flight feather molt. That none does suggests that HY Arctic Terns probably do not start flight feather molt before reaching the wintering grounds.

At least some subadults are known to accompany adults into the wintering grounds (Cramp 1985, Parmelee 1977; this study, USNM 394707, 394708), and adult birds are known to have reached pack ice as early as October (Cramp 1985). Therefore, a delayed or protracted migration period may have created a delay in the molt for those specimens collected after 8 October but not yet on the wintering grounds. A delayed or protracted migration period may also explain why some subadult birds have been observed replacing a large number of primaries at once (Parmelee 1977; this study, BM[NH] 44.1.1829). Delays in reaching the wintering grounds would reduce the time available for molt and so predictive cue(s) for regulating the end of molt (Hahn et al. 1992) might necessarily have forced more feathers to be replaced at once. Experimental manipulation of environmental factors has been shown to decrease the interval between the molting of primaries and to increase the rate of replacement (Chilgren 1978, Moore et al. 1982). This would suggest that subadults may be energetically incapable of replacing all flight feather tracts concurrently, and must instead replace them sequentially. If tracts are replaced sequentially by subadults, this would serve to explain why rectrices are still being replaced well into June (Table 2).

While it seems first flight feather molt is not initiated until HY birds reach the wintering grounds, banding records indicate that subadults can be found year-round off the coasts of South America and Africa (Cramp 1985, Morant et al. 1983) making it unclear as to whether or not individuals actually return to the wintering grounds before initiating the second flight feather molt. Although all subadults in the early stages of flight feather molt were found in the wintering range, it appears that at least some birds leave the wintering grounds prior to completing flight feather molt (Table 2; all June specimens still molting rectrices were collected in the migratory range). Because subadults are estimated to begin molt so much earlier than adults, and take twice the time to replace flight feathers, subadults may be under less time constraint to molt flight feathers than adults (due to the time involved in breeding and migration).

Adult Arctic Terns reach the wintering grounds before beginning flight feather molt. With individuals arriving on the wintering grounds as early as October, and leaving on northward migration as early as March (Cramp 1985), the molt duration estimate of just over three months, which is certainly skewed due to few data points from early in the molt period,

nevertheless fits well within estimates of the up to eight months being spent in migration and breeding efforts.

Despite the limited time available to molt, several specimens were found to be undergoing the second inner primary molt exhibited by most *Sterna* species (Cramp 1985, Stresemann and Stresemann 1966). Differential wear such that inner primaries become more worn than outer primaries has been argued as the reason for the two molts of inner primaries (Stresemann and Stresemann 1966). Given that only a few months are spent molting, it is unlikely that Arctic Terns replace inner primaries twice on the wintering grounds due to wear. Indeed, if differential wear were driving two primary molts in this genus, we should expect that the outer not inner primaries should be replaced twice because outer primaries wear more quickly (Jenni and Winkler 1994, Langston and Rohwer 1995).

If this pattern of replacement is widespread in Arctic Terns, it has gone unnoticed due to two factors. First, Arctic Terns do not molt some number of inner primaries while still on the breeding grounds, as many other species of *Sterna* do (Cramp 1985, Stresemann and Stresemann 1966). Second, the second replacement occurs so quickly, in fact overlapping in time the end of the first replacement, that no color contrast is evident between inner and outer primaries, as is easily visible on breeding individuals of other species. If this color contrast is a measure of quality for mate choice in those species that exhibit it (Voelker, submitted manuscript), then the inability of Arctic Terns to express this signal might be due to time constraints imposed by the length of breeding and migratory periods. Indeed, Arctic Terns may be phylogenetically constrained to feature such a molt; alternatively, the contrast may have been suppressed recently, as the length of migration increased following range expansion into higher latitudes following the most recent glacial retreats in the northern hemisphere. Also interesting is the head molt pattern displayed by this species. Data presented here indicate that the prebasic head molt is a partial molt, wherein only a limited number of black crown feathers are replaced by white feathers, while the prealternate head molt seems complete with all crown feathers replaced with new black feathers. This finding contradicts previous accounts, which imply that the head molt is complete (e.g., Cramp 1985). Because most tern species carry a mottled crown in basic (nonbreeding) plumage (see Harrison 1983), we should, if previous accounts are correct, find birds collected in migration or shortly thereafter that are replacing both black and white feathers on their heads. This would indicate that the head molt was complete. If other *Sterna* achieve a mottled crown in the same way that Arctic Terns seem to, we should only find white feathers being grown after breeding. Regardless of how the pattern of crown feather replacement is achieved, the mottled crown effect has interesting implications for the function of the nonbreeding crown plumage in terns (Voelker 1996).

ACKNOWLEDGMENTS

I am grateful to D. F. Parmelee for inspiring both this project and my interest in collections. S. Rohwer provided invaluable guidance throughout all phases of the study, without which

my ability to interpret molt in the larger context of life-history would have been undeveloped. I was supported by a Burke Museum Eddy Graduate Fellowship during portions of this project. J. Broughton, N. Hillgarth, R. Huey, N. Langston, M. Leu, G. Orians, T. Slagsvold, and C. Thompson contributed many helpful and insightful comments on the manuscript. The manuscript benefitted immensely from discussions with C. Wilds. J. Herron helped with the statistics. I am grateful to the following museums and their curators, collections managers and staff for the loan of Arctic Tern specimens under their care: Academy of Natural Sciences, Philadelphia, American Museum of Natural History (AMNH), Australian Museum (AM), British Museum (Natural History) (BM[NH]), Canadian National Museum of Natural Sciences (NMCAN), Durban Museum (South Africa), East London Museum (South Africa), Institut Royal des Sciences Naturelles (Belgium), Natural History Museum of Los Angeles County, Louisiana State University Museum of Natural Science, Museum Alexander Koenig (Bonn), Museum of Comparative Zoology, Museum National d'Histoire Naturelle (Paris), University of Kansas Museum of Natural History, University of Michigan Museum of Zoology, Museum of Vertebrate Zoology, National Museum of Victoria (Australia), National Museum of New Zealand, San Diego Society of Natural History, National Museums of Scotland, Queen Victoria Museum (Australia), Naturmuseum Senckenberg (Frankfurt), South African Museum, South Australian Museum, Transvaal Museum, University of Nevada at Las Vegas, U.S. National Museum of Natural History (USNM), University of Washington Burke Museum, Western Foundation of Vertebrate Zoology, Zoologisk Museum (Copenhagen).

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Received 17 Apr. 1996; accepted 8 Oct. 1996.