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MOLT OF BLACK BRANT (*BRANTA BERNICLA NIGRICANS*) ON THE ARCTIC COASTAL PLAIN, ALASKA

ERIC J. TAYLOR[1]
Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843, USA

ABSTRACT.—I examined patterns and chronology of the prebasic molt and primary-feather growth rate of nonbreeding and postbreeding Black Brant (*Branta bernicla nigricans*) on the Arctic Coastal Plain, Alaska. I estimated molt intensity for adults and subadults of both sexes with molt rate (MR, proportion of feathers in blood quills) and percent new feathers (PN, proportion of feathers that recently completed growth) for 26 feather tracts. I then calculated mean total molt score (TMS) and mean total percent new score (TPN) for each sex, age class, molt stage (arrival, start, early, mid-, and late molt), and Julian date. TMS increased from arrival to early molt (14 June–22 July). Subadults molted at greater intensity than did adults during early, mid- and late molt (20 July–1 August); however, males and females in both age classes did not differ. TPN scores were significantly ($P < 0.05$) greater from 25 July to 1 August than from 20 to 22 July, primarily as a result of maturation of remiges and wing coverts. Brant replaced body and wing feathers concurrently. Back, rump, breast, and side regions were comprised of 25% or more blood quills in adults to 50% or more blood quills in subadults during the flightless period. Brant departing the molt area completed growth of only 11 to 21% of all feathers. Ninth-primary growth rate ($\bar{x} = 7.2 \pm$ SE of 0.1 mm/day) did not vary over sex and age classes nor between years (1988 vs. 1989). Remex growth rate declined significantly ($P < 0.001$) through molt but was not related to Julian date nor initial body mass. Most Black Brant began remex growth 4–10 July; however, some postbreeding adults did not arrive and start molt until 24–25 July. Brant made short flights when the ninth primary averaged 62% of its mean final length; sustained flight occurred at about 70% of completed growth. The duration of flightlessness was 23 and 24 days for females and males, respectively. Flightless Black Brant were present in the Teshekpuk Lake molting area from 26 June through 19 August. Upon regaining flight ability, Black Brant moved to coastal staging areas. The chronology and intensity of feather replacement for Black Brant may be important when determining the appropriate management of habitats where molt occurs, especially when these are disturbed by human activities. *Received 16 August 1994, accepted 27 January 1995.*

THE POSTBREEDING PERIOD for migratory waterfowl is between reproduction and fall migration (Hohman et al. 1992; but see Fredrickson and Drobney 1979). During this stage, most ducks and geese molt wing and body feathers (Palmer 1976, Hohman et al. 1992:app. 5-1) and, subsequently, store adequate nutrient reserves for fall migration. Because postbreeding anatids are secretive and usually seek protective and inaccessible habitats during flightlessness (Fredrickson and Drobney 1979), little is known about the chronology, duration, or intensity of remigial molt.

Brood-rearing geese initiate remigial molt two to three weeks after their young hatch (Barry 1962, Owen and Ogilvie 1979). Failed breeders and nonbreeders often migrate to specific molting areas presumably to: (1) decrease the risk of predation and avoid human disturbance (Sterling and Dzubin 1967); (2) avoid competition with successful breeders molting on nesting areas (Salomonsen 1968); and/or (3) forage on higher-quality vegetation available at earlier growth stages in northern areas (Owen and Ogilvie 1979).

In Black Brant (*Branta bernicla nigricans*), failed breeders and nonbreeders migrate from nesting areas along the Yukon and Kuskokwim river deltas (Alaska), the Canadian Arctic, and the Chukotski Peninsula (Russia) to the Teshekpuk Lake molting area on the Arctic Coastal Plain of Alaska (Derksen et al. 1979, 1982). Teshekpuk

[1] Present address: Texas Parks and Wildlife Department, J. D. Murphree Wildlife Management Area, 10 Parks and Wildlife Drive, Port Arthur, Texas 77640, USA.

Lake lies within the boundaries of the National Petroleum Reserve and supports 8,000 to 32,000 Black Brant, 5,000 to 27,000 Canada Geese (*Branta canadensis*), 1,000 to 7,000 White-fronted Geese (*Anser albifrons*), and 100 to 700 Lesser Snow Geese (*Chen caerulescens caerulescens*; Derksen et al. 1979). The U.S. Department of Interior designated the area surrounding Teshekpuk Lake as a Special Area, thereby temporarily suspending petroleum development (U.S. Department of Interior 1977). However, activities associated with future petroleum exploration could threaten Coastal Plain wetland habitats used by molting waterfowl (Derksen et al. 1979, 1982, Hohman et al. 1992). Aircraft disturbance caused flightless Black Brant to be alert, to be evasive (running, swimming, flightless flapping), or to leave preferred molting sites (Derksen et al. 1979, 1982, Jensen 1990). Moreover, molting Black Brant (Jensen 1990), like wintering Brent Geese (*Branta bernicla*) in England (Owens 1977) and Pink-footed Geese (*Anser brachyrhynchus*) in Denmark (Madsen 1985), do not habituate to helicopter disturbance.

The molting pattern, molting chronology, and feather-growth rates have not been adequately described in Anserinae (Hohman et al. 1992, Gates et al. 1993). Little is known about factors (e.g. photoperiod, migration chronology, nutritional status) influencing molt of nonbreeding and postbreeding geese, and the extent and sequence of body feather molt in relation to remigial molt is poorly understood (Derksen et al. 1982, Hohman et al. 1992, Gates et al. 1993). Although Derksen et al. (1979, 1982) used aerial and ground surveys to estimate the chronology and duration of flightlessness in Black Brant, they did not examine molt and remex regrowth in relation to age, sex, and breeding status. I conducted research to answer questions regarding the prebasic molt of wing and body feathers, and to address management and conservation issues. My goals in studying Black Brant at the Teshekpuk Lake molting area were to: (1) characterize the chronology, intensity, and variability in remigial and body-feather molt; (2) estimate primary-feather growth rate; and (3) examine chronology and duration of molt as influenced by age, sex, and breeding status.

Study Area and Methods

The Teshekpuk Lake study area lies on the Arctic Coastal Plain of Alaska. Large, NNW-SSE oriented thaw lakes together with low- and high-center polygons, comprise 50 to 75% of the Coastal Plain (Black and Barksdale 1949, Hussey and Michelson 1966). Derksen et al. (1981, 1982) described shoreline habitats of the principal study site located at Island Lake (70°39′N, 153°15′W).

I collected Black Brant at the Island Lake study area between 14 June and 5 August in 1988 and 1989. Birds were frozen within 24 h of collection and later transported to Texas A&M University. In the laboratory, I sexed specimens by cloacal examination. The presence of white-tipped middle wing coverts indicated second-year (SY) or subadult Black Brant (Harris and Shepherd 1965). The absence of white-tipped coverts in conjunction with a sheathed penis (males) and/or brood patch (females) indicated postbreeding, after-second-year (ASY) Black Brant (i.e. birds in at least their third summer). I excluded locally nesting Black Brant to restrict analyses to nonbreeders and failed nesters. Locally breeding females had developing follicles, oviducal eggs, or a bare brood patch. I considered locally breeding males as those collected in the presence of a potential mate, and that had testes larger than 17 × 9 mm. I classified males with testes larger than 17 × 9 mm, which were collected in a feeding flock or without an apparent mate, as failed nesters and included them in the molt sample. Overall, I analyzed 100 ASY (60 males, 40 females) and 79 SY Black Brant (41 males, 38 females)

I categorized Black Brant in five molt stages: (1) *arrival*, Black Brant collected prior to the start of remex molt; (2) *start of molt*, ninth-primary length 0–19% ($\bar{x}$ = 10%) of mean final length, where mean final length was 223 and 214 mm for ASY males and ASY females, respectively; (3) *early molt*, ninth primary 20–45% ($\bar{x}$ = 37%) of mean final length; (4) *midmolt*, ninth primary 46-60% ($\bar{x}$ = 53%) of mean final length; and (5) *late molt*, ninth primary more than 60% ($\bar{x}$ = 66%) of mean final length. I selected ninth-primary percentages (and molt stages) *a priori* to approximate previously reported values (Ankney 1984) and to maintain adequate sample sizes among molt stages.

The proportion of blood quills typically is the number of exposed quills on the inner side of the skin scraped free of fat (see Oring 1968). However, because I required the skin, subcutaneous fat, and remainder of the carcass for lipid analyses, I exposed feather sheaths (calamus and inferior umbilicus) of contour feathers using a dissecting probe. I estimated molt rate (MR) as the proportion of contour feathers in the blood-quill stage, and percent new (PN) as the proportion of new feathers that had recently completed growth in each of 26 feather tracts (see Billard and Humphrey 1972, Young and Boag 1981, Miller 1986).

I defined a blood quill as any new, emerging contour feather containing blue color within the shaft. I considered feather sheaths at or slightly above the skin surface, and missing rectrices and remiges, as blood quills. I scored MR and PN for each feather

TABLE 1. Regression equations to predict ninth-primary feather insertion length (Y) for 1988 data based on 1989 wing length (W) and ninth-primary feather-tip length (T) data.

Prediction[a]	Equation	R^2
	ASY-M (n = 574)	
1	$Y = -77.5 + 0.67W + 0.40T$	0.97
2	$Y = -135.8 + 1.02W$	0.96
	ASY-F (n = 432)	
1	$Y = -47.3 + 0.48W + 0.68T$	0.95
2	$Y = -131.1 + 1.02W$	0.91
	SY-M (n = 159)	
1	$Y = -54.2 + 0.54W + 0.53T$	0.97
2	$Y = -137.2 + 1.03W$	0.94
	SY-F (n = 152)	
1	$Y = -44.3 + 0.48W + 0.66T$	0.93
2	$Y = -135.6 + 1.05W$	0.90

[a] Prediction 1 based on wing length and ninth-primary feather-tip length, while prediction 2 based only on wing length.

tract from 0 to 4: (0) 0%; (1) 1–25%; (2) 26–50%; (3) 51–75%; and (4) 76–100%. I combined feather tracts to groups based on eight regions (Billard and Humphrey 1972, Miller 1986): (1) head and neck (crown, facial, chin/throat, and neck); (2) back and rump (upper and lower back, scapulars, rump); (3) breast (belly, chest tracts); (4) side (side, flank); (5) outer wing coverts (outer lesser, middle, primary, and secondary coverts); (6) remiges (primaries, secondaries, tertials); (7) inner wing coverts (inner lesser, middle, primary and secondary coverts); and (8) tail (rectrices, upper and lower tail coverts). I calculated the mean MR- and PN-region scores as:

$$\bar{x} = \Sigma\, x/(n_f n_b), \qquad (1)$$

where $\bar{x}$ is the average MR- or PN-region score, x is an individual MR or PN score, n_f is the number of feather tracts within a region, and n_b is the number of birds examined within a group (e.g. by age, sex, molt stage, or feather region). The maximum mean MR or PN region score is 4. Because I collected arrival Black Brant from 14 June to 15 July, and remigial molt began from 26 June to 25 July, molt stages overlapped; therefore, I could not define changes in molt pattern relative to calendar-date intervals.

I calculated the total molt scores and total percent-new scores by summing all feather tract MR or PN scores for each bird, with the maximum score being 104 ([score of 4] × [26 feather tracts] = 104). I determined the mean total molt score (TMS) and mean total percent-new scores (TPN) for each sex, age class, molt stage, and Julian date range. I examined TMS and TPN scores across sex and age classes with a 2 × 2 factorial analysis of variance (ANOVA), and across molt stages and dates with an ANOVA. When a significant F-value was found, I evaluated differences in means with a Tukey's HSD test (see Young and Boag 1981). I compared the mean number of rectrices across molt stages with ANOVA, and across sex and age classes with a 2 × 2 factorial ANOVA. Means were compared using contrasts. All statistical procedures were conducted using SAS (SAS Institute 1985).

I assessed ninth-primary growth rate by trapping flightless Black Brant on six lakes during 10–29 July in 1988 and 1989. In 1988, I measured most ninth-primary feathers (mm) from the distal edge of the blue blood quill (sheath) to the feather tip; I did not measure emerging ninth-primary blood quills without exposed feather tips. Blood-quill distal edges began to slough off as remiges matured, producing a variable reference point to determine length. In 1989, I measured both the feather-tip length and the insertion or total length (defined as distance from insertion of remex blood quill at skin surface to distal end of feather tip; Hanson 1962, Gates et al. 1993). I recorded the flattened wing length (distance from blunt end of wrist joint to distal tip of longest primary; mm) in 1988 and 1989. Two regression equations for each age and sex group based on the 1989 data set were developed to predict the primary insertion length for the 1988 data set (Table 1).

I estimated the ninth-primary growth rate (mm/day) for molting Black Brant banded and recaptured during the same summer in both 1988 and 1989. I calculated daily growth rate (G) as:

$$G = (L_B - L_R)/t, \qquad (2)$$

where L_B is the initial ninth-primary length at banding, L_R is the length at recapture, and t is the time in number of days between banding and recapture. I tested for potential differences in primary-growth rate between sex and age classes with ANOVA, and between years (1988 vs. 1989) with a t-test. I regressed feather-growth rates against initial ninth-primary length, Julian date, and initial body mass.

Primary growth rates of six ASY (three male, three female) captive Black Brant were recorded from 10 through 29 July 1989. The birds fed on natural grasses, sedges, forbs, game-bird chow, and oyster-shell grit. I recorded primary lengths at 4- to 10-day intervals.

The start date of remex growth (i.e. primary length = 0 mm) was estimated by dividing the mean ninth-primary length recorded during the first banding drive in 1988 (10 July) and 1989 (12 July) by the mean primary growth rate; the number of growth days was subtracted from the two banding dates to estimate the start date of remex growth.

RESULTS

Body- and wing-molt pattern.—Brant had not started wing molt before arriving on the molting area (Figs. 1–4). Body molt was light (MR $\bar{x}$

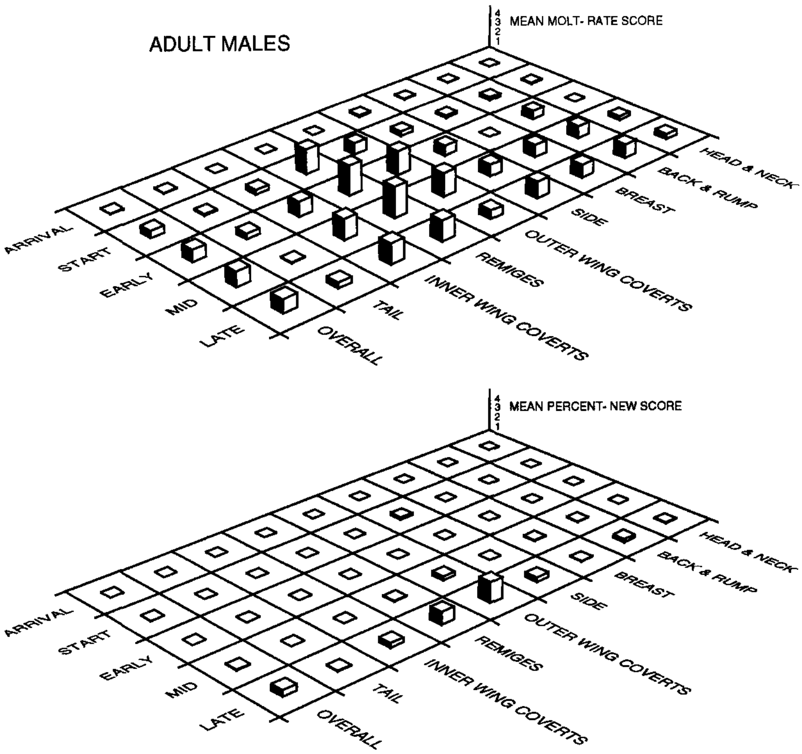

Fig. 1. Mean molt-rate and percent-new scores for adult male Black Brant from arrival through late molt.

< 1) in all Black Brant except for on the sides of SY males (MR $\bar{x} = 1.6$; Fig. 3) and breasts (old brood patches) of ASY females (MR $\bar{x} = 1.8$; Fig. 2). ASY males had the lowest overall mean MR score. ASY Black Brant did not complete growth of new feathers (PN $\bar{x} = 0$) in any region (Figs. 1 and 2), although SY Black Brant had new, fully emerged feathers in the breast, side and tail regions (Figs. 3 and 4).

During the start of molt, all Black Brant initiated remigial and covert (predominantly outer primary, outer secondary and outer lesser; Figs. 5 and 6) molt. SY males and ASY females continued to replace feathers in the side and breast regions, respectively. The mean PN scores approximated those at arrival.

Blood quills comprised about 75% of remiges (MR $\bar{x} = 3.9$; Figs. 1–4) at early molt. Molt of outer wing coverts peaked as blood quills formed 75 to 100% (MR $\bar{x} = 4.0$) of the primary and secondary coverts and 50 to 75% (MR $\bar{x} \geq 3$) of the lesser coverts. Black Brant replaced inner wing coverts, predominantly secondaries (Figs. 5 and 6). SY males continued replacing side feathers (MR $\bar{x} = 3.0$). About 25% of the breast region (brood patch) of ASY females contained new feathers that had completed growth.

During midmolt, overall mean MR scores peaked for ASY males, ASY females, and SY males as the result of remex and outer wing covert molt. Similar to early molt, outer primary, secondary, and lesser coverts, and inner secondary coverts contained the greatest percentage of blood quills. Back and rump, breast, and inner wing covert mean MR scores increased relative to early molt. The breast region of ASY females contained the greatest proportion of completed new feather growth (PN $\bar{x} = 2.8$).

Overall mean MR scores in late molt declined for ASY males, ASY females, and SY males as new remiges and outer wing coverts completed growth. The overall mean MR score peaked for SY females because mean MR scores for six out of eight feather regions ranked highest among the four age/sex groups. The inner wing covert mean MR scores increased (SY brant) or remained at their maximum (ASY brant). Replacement of outer middle and inner primary coverts lagged behind that of other coverts. Mean PN

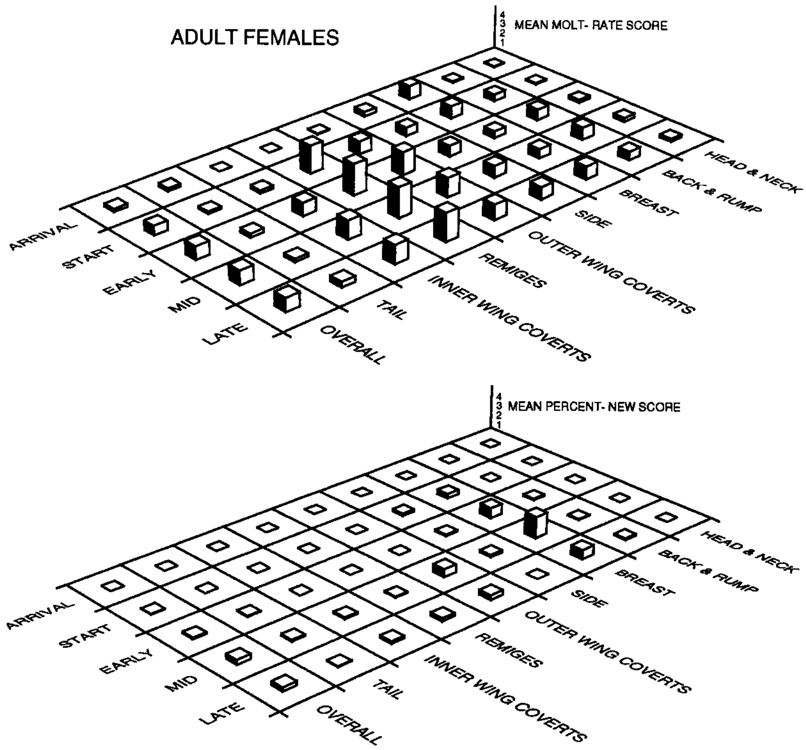

Fig. 2. Mean molt-rate and percent-new scores for adult female Black Brant from arrival through late molt.

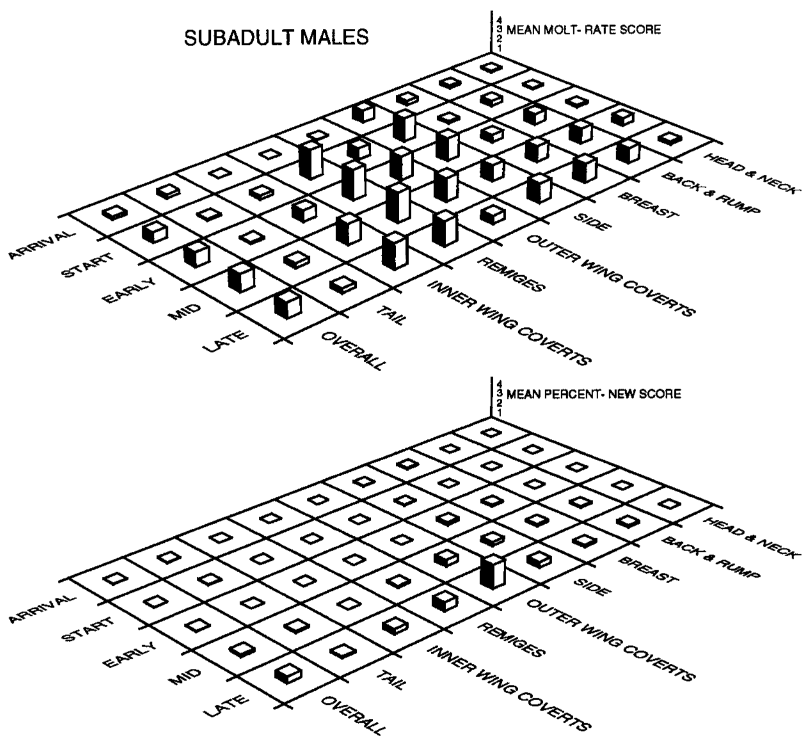

Fig. 3. Mean molt-rate and percent-new scores for subadult male Black Brant from arrival through late molt.

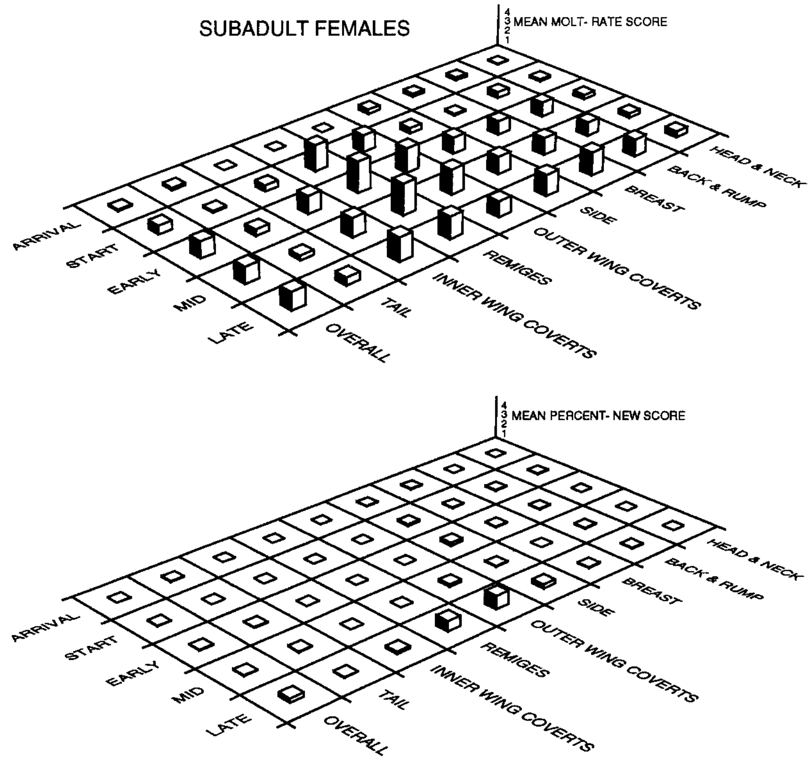

Fig. 4. Mean molt-rate and percent-new scores for subadult female Black Brant from arrival through late molt.

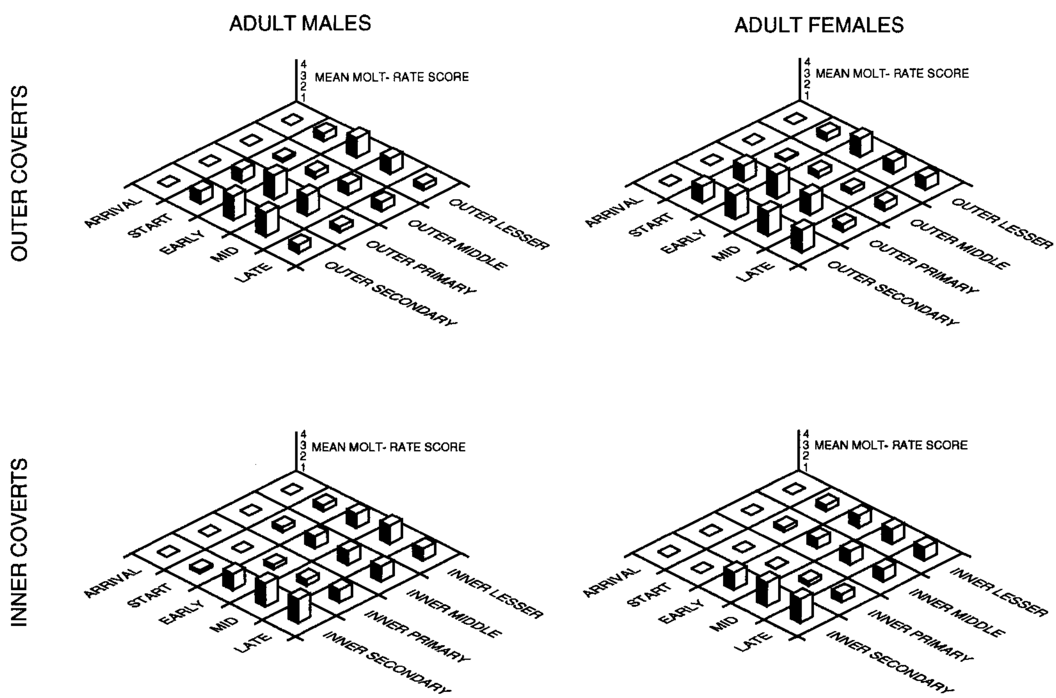

Fig. 5. Mean molt-rate scores of outer and inner wing coverts for adult male and adult female Black Brant from arrival through late molt.

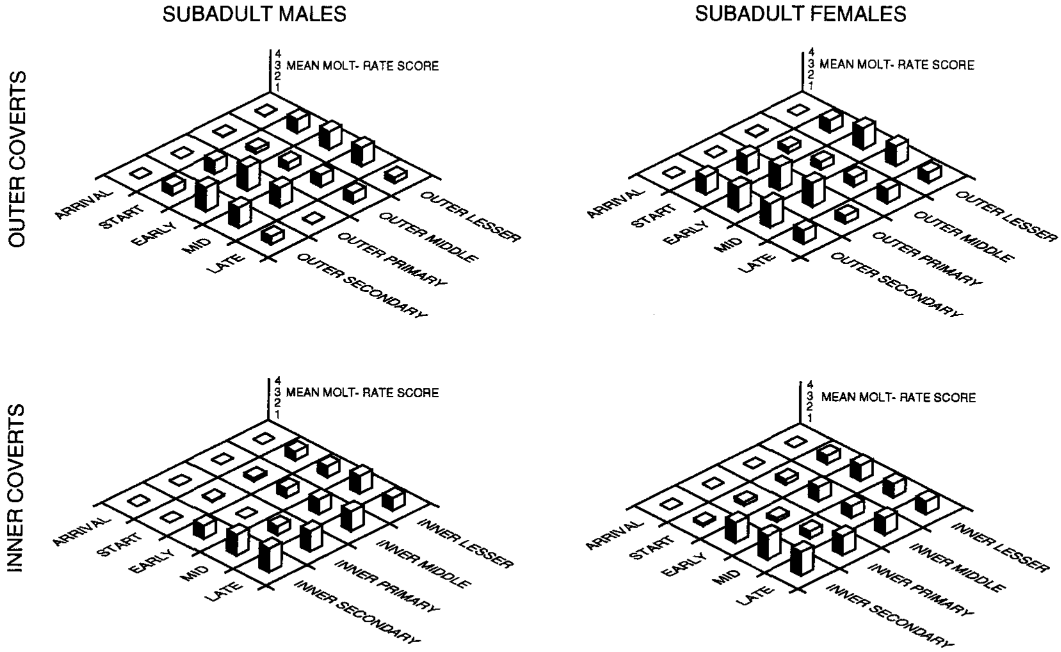

Fig. 6. Mean molt-rate scores of outer and inner wing coverts for subadult male and subadult female Black Brant from arrival through late molt.

scores for SY and ASY males (both 0.8) exceeded those for ASY and SY females (both 0.5).

Mean total molt score (TMS).—As a result of remex molt, TMS scores at the start of molt exceeded significantly ($P < 0.05$) those at arrival (Table 2). TMS scores from early to late stages were statistically equal, but exceeded those during the start of molt. Results of age and sex factorial analyses varied by molt stage. The age × sex interaction was only significant ($P < 0.01$) during arrival. TMS scores in SY Black Brant were higher than ASY brant during early molt ($P < 0.05$), midmolt ($P < 0.05$), and late molt ($P = 0.08$). There were no differences in TMS scores between sexes except during early molt (F > M, $P < 0.05$).

TABLE 2. Mean total molt scores (TMS) of adult (ASY), subadult (SY), male (M), and female (F) Black Brant. Scores underlined with same line not statistically different ($P > 0.05$). Lack of common underscore indicates that TMS differed significantly ($P < 0.05$; Tukey's HSD multiple-comparison test).

Age and sex	Molt stage				
	Arrival	Start	Early	Mid-	Late
ASY-M	1.4	22.4	40.3	48.1	42.4
ASY-F	6.2	29.8	42.1	46.5	43.0
SY-M[a]	6.2	26.2	42.0	55.7	46.1
SY-F	4.7	29.0	53.8	55.0	55.0

[a] Early and late underscored with same line, as are mid- and late.

To determine the chronology and intensity of molt with respect to date, I examined TMS scores during four periods (selected to equalize sample sizes among sex and age classes): 14 June–15 July (arrival), 4–19 July, 20–22 July, and 25 July–1 August (Table 3). Because wing molt had not started and body molt was minimal, arrival TMS scores were significantly less than during 4–19 July. TMS scores increased through 20–22 July and remained unchanged during the 25 July–1 August period except for SY males, where TMS scores declined significantly. TMS scores of SY birds were higher than those of ASY birds during the last two periods examined: 20–22 July ($P < 0.01$) and 25 July–1 August ($P < 0.05$), but did not differ 4–19 July ($P = 0.67$). TMS scores of males and females were not different during the latter three time periods.

Mean total percent-new score (TPN).—Late-molt TPN scores exceeded those of arrival, start, early, and midmolt, except in ASY females (Table

TABLE 3. Mean total molt scores (TMS) of Black Brant by date. Scores underlined with same line not significantly different ($P > 0.05$). Lack of common underscore indicates TMS differed significantly ($P < 0.05$; Tukey's HSD multiple-comparison test). See Table 2 for definitions.

Age and sex	Time period			
	14 June–15 July[a]	4–19 July	20–22 July	25 July–1 August
ASY-M	1.4	24.1	46.6	42.7
ASY-F	6.2	31.0	44.2	43.2
SY-M	6.2	29.8	55.2	45.5
SY-F	4.7	29.0	55.7	52.7

[a] Arrival.

TABLE 5. Mean total percent-new scores (TPN) of Black Brant by date. Scores underlined with same line not statistically different ($P > 0.05$). Lack of common underscore indicates TPN differed significantly ($P < 0.05$; Tukey's HSD multiple-comparison test). See Table 2 for definitions.

Age and sex	Time period			
	14 June–15 July[a]	4–19 July	20–22 July	25 July–1 August
ASY-M	0.0	0.6	4.4	15.6
ASY-F	0.0	2.1	5.7	11.6
SY-M	0.8	1.3	3.6	16.6
SY-F	0.8	1.3	1.6	11.1

[a] Arrival.

4). Arrival TPN scores differed significantly ($P < 0.001$) between age classes (SY > ASY). TPN scores varied between sexes (M > F) only during the late molt. TPN scores during 25 July–1 August exceeded those during all previous dates (Table 5), similar to results based on molt stage. Age and sex effects and the age × sex interaction of TPN scores within the latter three time periods were not significant.

Rectrix molt.—Both the percent frequency (Table 6) and intensity (Fig. 7) of rectrix molt increased in later molt stages. New rectrices occurred most often in SY females followed by SY males and ASY females. Only 3% of 60 ASY males incurred any tail molt during the flightless period. Rectrix molt pattern (recorded for 21 of 29 Brant molting one or more rectrices) indicated feathers were generally replaced in a symmetrical pattern (Fig. 8).

Of 125 Black Brant examined for rectrix number (i.e. number of old, new, and blood-quill feathers), 80 (64%) had 16 rectrices, 26 (21%) had 15, 7 had 17, 5 had 14, 5 had 18, and 1 each had 13 and 10. The mean number of rectrices for ASY males (15.9 ± 0.2, $n = 40$), ASY females (15.7 ± 0.1, $n = 29$), SY males (16.1 ± 0.2, $n = 30$), and SY females (15.4 ± 0.3, $n = 26$) differed between SY Black Brant only (M > F; $P < 0.05$). The numbers of rectrices examined across molt stages (arrival to late molt) were not significantly different: ASY males ($F = 1.06$, $P = 0.39$), ASY females ($F = 0.71$, $P = 0.60$), SY males (F

TABLE 4. Mean total percent-new scores (TPN) of Black Brant across stage of molt. TPN scores underlined with same line not statistically different ($P > 0.05$). Lack of common underscore indicates that TPN differed significantly ($P < 0.05$; Tukey's HSD multiple-comparison test). See Table 2 for definitions.

Age and sex	Molt stage				
	Arrival	Start	Early	Mid-	Late
ASY-M	0.0	0.6	0.0	2.9	21.2
ASY-F	0.0	1.8	4.1	11.7	11.8
SY-M	0.8	0.5	1.3	6.5	21.3
SY-F	0.8	1.3	1.8	2.0	13.7

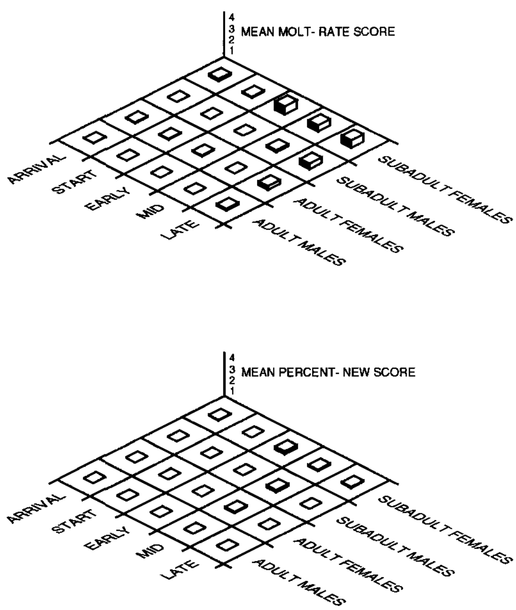

Fig. 7. Mean molt-rate and percent-new scores of rectrices for Black Brant from arrival through late molt.

TABLE 6. Percent frequency and number of Black Brant that molted rectrices (as indicated by missing and/or presence of blood quills) from arrival through late-molt stages (see Table 2 for definitions).

Stage	Age/sex group					
	ASY-M	ASY-F	SY-M	SY-F	Total	Percent
Arrival	1/27	0/10	0/11	2/10	3/58	5.2
Start of molt	0/8	1/9	0/6	1/8	2/31	6.3
Early molt	0/3	1/9	0/6	6/8	7/26	26.9
Midmolt	0/11	0/6	3/11	4/6	7/34	20.6
Late molt	1/11	3/6	3/7	3/6	10/30	33.3
Total	2/60	5/40	6/41	16/38	29/179	16.2
Percent	3.3	12.5	14.6	42.1	16.2	

= 0.66, P = 0.63), and SY females (F = 0.89, P = 0.49).

Remex molt and growth rate.—Primary and secondary remiges molted at about the same time. However, distal primaries (nos. 6-10) dropped prior to proximal ones (nos. 1-5), whereas proximal secondaries were molted first. The tenth primary emerged prior to the ninth primary, and exceeded it in length until the ninth reached approximately 15% (≈34 mm) of its total length. As molt progressed, proximal primaries reached their total length earlier than did distal primaries, and secondaries attained final length earlier than primaries (Table 7). When the ninth-primary length ranged from 151 to 180 mm, an average of only 5 primaries had completed growth compared to 10 secondaries.

Estimation of the primary-feather growth rate was based on 247 Black Brant (1988 and 1989 combined) recaptured during the summer of

TABLE 7. Number and location of fully emerged (based on clear rachis color) primary and secondary feathers of Black Brant (collected July-August 1988-1989) with at least one fully emerged remex.

Bird no.	Ninth-primary length (mm)	Remige location[a]									
		1	2	3	4	5	6	7	8	9	10
1	120	●	●	●							
2	121	●○	●○	●○	●○	●○	○	○	○	○	○
3	128	●○	●○	●○	●○	●○	○	○	○	○	○
4	129	●○	●○	●○	●○						
5	130	●									
6	131	●									
7	133	●○	●○	●○	○	○	○	○	○	○	○
8	134	●○	●○								
9	134	●○	●○	●○	●○	●○	○	○	○	○	○
10	136	●	●								
11	140	●○	●○	●○	○	○	○	○	○	○	○
12	141	●○	●○	●○	○	○	○	○	○	○	○
13	143	●○	●○	●○	●○	○	○	○	○	○	○
14	145	●○	●○								
15	145	●○	●○	●○	○	○	○	○	○	○	○
16	145	●○	●○	●○	○	○	○	○	○	○	○
17	147	●○	●○	●○	○	○	○	○	○	○	○
18	148	●○	●○	●○	○	○	○	○	○	○	○
19	150	●○	●○	●○	●○	●○	●○	○	○	○	○
20	151	●○	●○	●○	●○	●○	●○	○	○	○	○
21	152	●○	○	○	○	○	○	○	○	○	○
22	155	●○	●○	●○	●○	○	○	○	○	○	○
23	156	●○	●○	●○	●○	○	○	○	○	○	○
24	174	●○	●○	●○	●○	●○	●○	●○	○	○	○
25	180	●○	●○	●○	●○	●○	●○	○	○	○	○

[a] ● primary; ○ secondary.

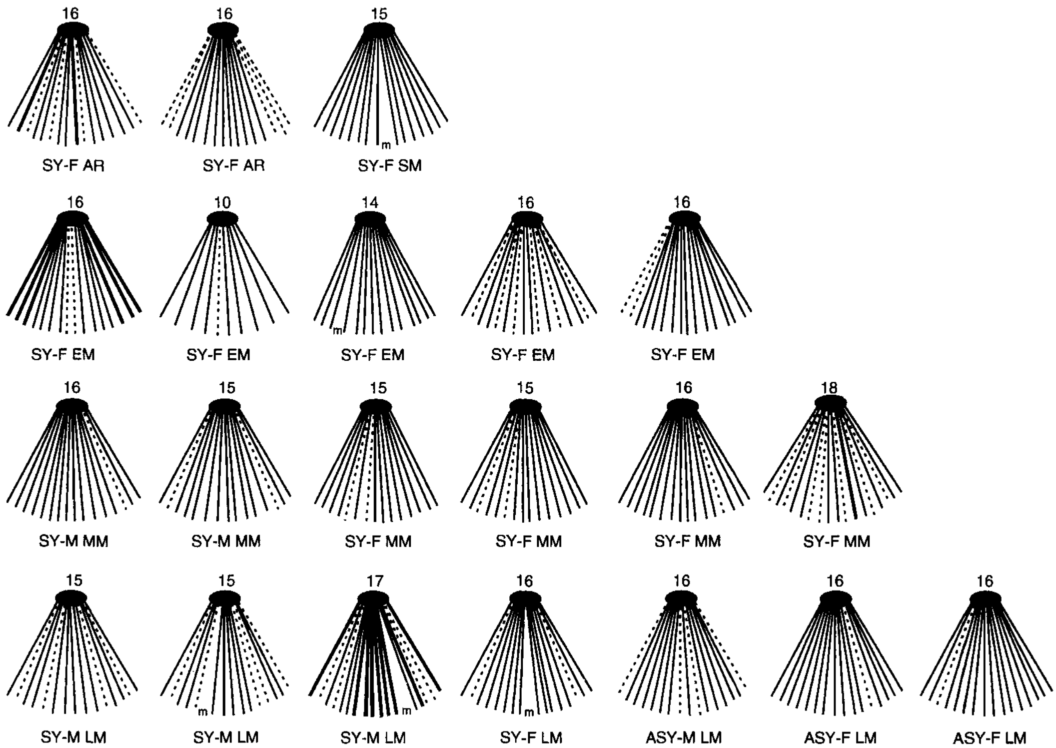

Fig. 8. Rectrix molt of adult male (ASY-M), adult female (ASY-F), subadult male (SY-M), and subadult female (SY-F) Black Brant during arrival (AR), start (SM), early (EM), mid- (MM), and late (LM) molt. Total number of rectrices present indicated above each subfigure. Solid thin line = old feather; dashed line = incoming blood quill; solid thick line = recently replaced feather; m = molted and not yet emerged.

banding. Of these, I recaught 231 (94 ASY male, 77 ASY female, 36 SY male, 24 SY female) once and 16 (5 ASY male, 9 ASY female, 2 SY female) twice. The interval between the first and second captures ranged from 1 to 16 days and averaged: ASY males, 6.6 ± 0.3; ASY females, 7.1 ± 0.3; SY males, 7.4 ± 0.4; and SY females, 6.7 ± 0.6.

The mean ninth-primary growth rate was 7.2 ± 0.1 mm/day. Ninth-primary growth rates derived when initial feathers measured ≥0 mm (i.e. when a delay in feather emergence may influence growth-rate calculations) or ≥1 mm did not differ across age and sex classes (age, $F = 0.22$, $P = 0.88$, $n = 247$; sex, $F = 1.10$, $P = 0.35$, $n = 226$). Overall (ages and sexes combined) growth rates of primaries in 1988 ($n = 98$) and 1989 ($n = 149$) did not differ ($\bar{x} = 7.2 \pm 0.1$ mm/day; $t = 0.51$, $P = 0.61$). The primary growth rate based on an initial ninth-primary measurement equaling 0 mm (i.e. no emergence) averaged 6.3 ± 0.3 mm/day ($n = 21$) was significantly ($t = -3.12$, $P < 0.01$) slower than the rate (7.3 ± 0.1, $n = 226$) calculated for primaries greater than or equal to 1 mm. The primary growth rate did not change in relation to Julian date ($P = 0.63$, Fig. 9A) or initial body mass ($P = 0.40$, Fig. 9B).

The mean primary growth rate of six captive Black Brant (derived from initial ninth primaries greater than or equal to 1 mm; $n = 19$) averaged 7.0 ± 0.3 mm/day. The primary growth rate (derived from initial ninth primaries greater than or equal to 1 mm) slowed ($P < 0.001$) as the length of the primary increased in both wild-trapped (Fig. 10A) and captive (Fig. 10B) Black Brant.

Molt chronology.—Assuming two days between feather drop and emergence (Boyd and Maltby 1980, Geldenhuys 1983, Panek and Majewski 1990), most Black Brant began primary molt during the first week in July (Table 8). However, some individuals were flightless by 26 June, and several ASY Brant began molt as late as 25 July.

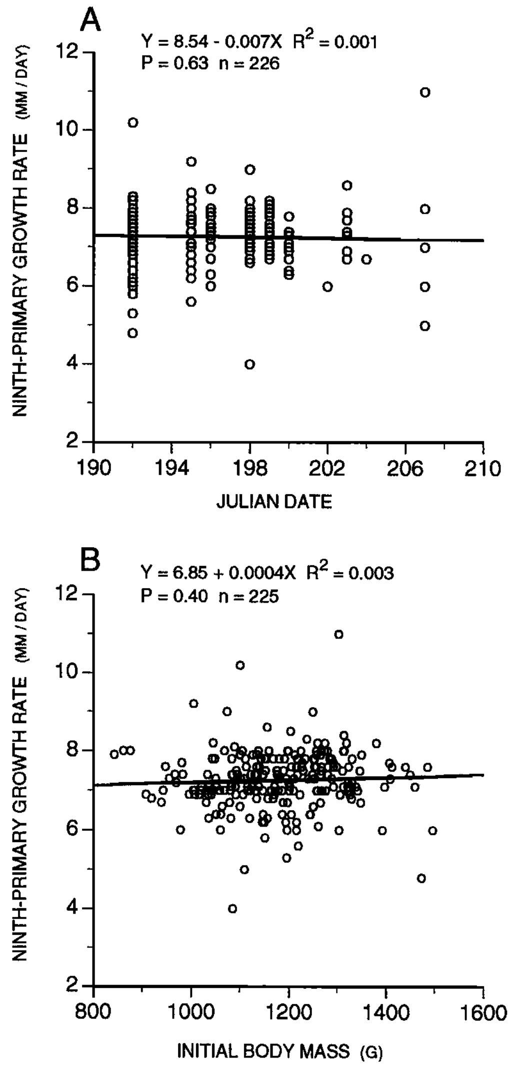

Fig. 9. (A) Ninth-primary growth rate regressed against Julian date (192, 195, 203 indicate 10, 13, 23 July 1988, respectively; 196, 198, 199, 200, 202, 207 indicate 15, 17, 18, 19, 21, 26 July 1989, respectively). (B) Ninth-primary growth rate regressed against initial body mass.

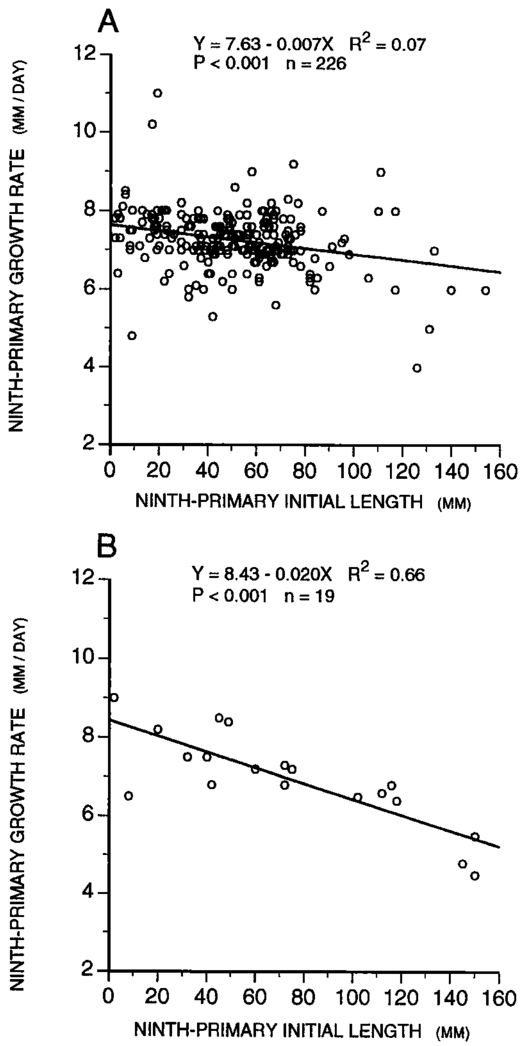

Fig. 10. (A) Ninth-primary growth rate of wild-trapped Black Brant regressed against ninth-primary initial length (length at first capture if ≥1 mm). (B) Ninth-primary growth rate of captive Black Brant regressed against ninth-primary initial length for feathers with initial lengths of 1 mm or more.

Black Brant began remex molt three to five days earlier in 1988 than in 1989 (Table 8). I estimated the ninth-primary length of Black Brant banded 12 July 1989 (Julian date 193) for 10 July 1988 (Julian date 192) by subtracting 7 mm (growth for one day) from the 1989 data. ASY males and ASY females had significantly ($P < 0.001$) shorter primaries on this date in 1989 than in 1988. The estimated 1989 primary lengths for SY males and SY females were not shown to be significantly shorter ($P = 0.11$ and 0.19, respectively) relative to this date in 1988; however, small samples and the distribution of data likely influenced results (3 of 8 SY males and 4 of 8 SY females had preadjusted primary lengths of 0 mm and, thus, could not be further corrected).

The maximum number of flightless birds occurred about 21 July. At this time, immigration

TABLE 8. Ninth-primary length and estimated molt initiation of Black Brant captured on 10 July 1988 (Julian date 192) and 12 July 1989 (193). Estimate provided for Julian date 192 in 1989 (see Table 2 for definitions).

Age and sex	Ninth-primary length (mm)	Molt initiation
	$\bar{x}$ ± SE(range[a], n)	$\bar{x}$(range[a])
	10 July 1988 (Julian date 192)	
ASY-M	46 ± 3 (0–100, 97)	4 July(26 June–25 July)
ASY-F	39 ± 3 (0–85, 59)	5 July(28 June–24 July)
SY-M	26 ± 3 (0–57, 42)	6 July(2–21 July)
SY-F	28 ± 4 (0–67, 19)	6 July(1–21 July)
	12 July 1989 (Julian date 193)	
ASY-M	27 ± 5 (0–100, 34)	8 July(28 June–25 July)
ASY-F	14 ± 3 (0–67, 42)	10 July(3–25 July)
SY-M	20 ± 7 (0–46, 8)	9 July(6–19 July)
SY-F	19 ± 11(0–88, 8)	9 July(30 June–21 July)
	Estimate for Julian date 192 in 1989	
ASY-M	22 ± 5 (0–93)	—
ASY-F	10 ± 2 (0–60)	—
SY-M	16 ± 5 (0–39)	—
SY-F	16 ± 10(0–81)	—

[a] Last date of molt initiation estimated from all banding records.

of late, postbreeding ASY Black Brant had ended, and only about 4% of all Black Brant had regained the ability to fly (see below). By 26–29 July, 9% of all molting Brant had flight capability.

Between 17–19 July and 21–22 July banding periods, the mean ninth-primary length of ASY Black Brant declined, while the mean ninth-primary length of SY Black Brant increased. This difference was likely the result of a late immigration of postbreeders. This supposition is supported by recent remex molt (ninth primary = 0 mm) for several ASY males and ASY females during 21–22 July, compared to the shortest SY ninth-primary length (16 mm). Also, prior to 17 July (1988 and 1989), the ninth-primary lengths of brood-patch ASY females and nonbrood-patch ASY females were not significantly different ($P > 0.05$) based on four banding dates on three lakes. However, from 17–27 July, the mean ninth-primary length of nonbrood-patch ASY females was significantly ($P < 0.05$) longer than brood-patch ASY females in six of nine comparisons. Finally, prior to 21 July, brood-patch ASY females comprised 53% (1988) and 60% (1989) of all ASY females. After 21 July, the brood-patch ASY females proportion increased to 82% and 78%, respectively.

I compared the molt chronology between/among sexes, age classes, and between breeders and nonbreeders (ASY females only) from one lake complex on 17–19 July 1989 (Table 9). Mean ninth-primary length of SY females and nonbrood-patch ASY females did not differ ($P > 0.05$); neither did SY males and ASY males. The mean ninth-primary length of nonbrood-patch ASY females exceeded ($P < 0.001$) that of brood-patch ASY females, as previously noted, for most banding dates after 17 July 1988 and 1989. Brood-patch ASY females also had shorter ($P < 0.01$) ninth primaries than SY females. Coefficients of variation were highest for brood-patch ASY females (Table 9), indicating that postbreeding ASY females were least synchronized in molt initiation. SY Black Brant began molt with greater uniformity than ASY Black Brant.

The availability of open water in early summer did not affect molting chronology. Based on three pairs of banding dates, primary lengths of ASY Brant molting on East Long and Island

TABLE 9. Statistics for ninth-primary lengths (mm) of Black Brant measured 17–19 July 1989.

Age and sex	n	Ninth primary	
		$\bar{x}$ ± SE	CV
ASY-M	268	88.5 ± 1.8	32.7
ASY-F[a]	83	65.2 ± 3.2	44.0
ASY-F[b]	64	84.3 ± 3.4	32.5
SY-M	87	84.3 ± 2.1	23.3
SY-F	70	76.5 ± 2.7	29.3

[a] Had brood patch (failed-nesting bird).
[b] No brood patch.

lakes were not different ($P > 0.05$), although East Long Lake became ice-free 7 to 14 days after Island Lake.

Flightless duration can be estimated from ninth-primary lengths of captured birds that flew upon release. Some Black Brant ($n = 36$) regained flight when the ninth primary averaged 62% (range 53-73%) of its definitive length; however, this estimate is potentially biased due to wind-aided flight, below average body mass, or handling stress. Black Brant with ninth primaries at this length had completed (on average) growth of only one to three primaries and five to seven secondaries. Sustained flight likely occurs when the ninth primary reaches about 70% of final length. Of 2,265 Brant trapped and banded, I captured only four males with primaries 156 mm or more in length and no females with primaries 150 mm or more in length.

Assuming a constant growth rate of 7.2 mm/day, the ninth primary requires 30 to 31 days to reach full length (ASY male = 223 mm; ASY female = 214 mm). Because two days pass between molt and emergence of remiges, and growth rate likely declines during late molt, the ninth primary could require 35 days to complete growth. However, if sustained flight occurs at 70% of the ninth-primary final length, the actual flightless period—including lag time (two days) and a slowed growth rate in late molt (overall mean growth rate estimated at 7.0 mm/day)—would equal 23 for females and 24 days for males.

To estimate when 50% of the population could fly, I used the mean ninth-primary length recorded 26-29 July, and added the number of days (based on 7 mm/day) required for the feather to reach 70% total length. By 2 August, 50% (ASY males), 52% (ASY females), 55% (SY-males), and 52% (SY females) of Black Brant could depart the molting area for coastal staging areas.

Discussion

Previous studies have suggested that body molt in Anserinae is delayed until after the flightless period (Cramp and Simmons 1977, Ankney 1984, Hohman et al. 1992, but see Gates et al. 1993). However, at Teshekpuk Lake, Black Brant replaced wing and body feathers concurrently. Body-molt intensity varied by feather tract and time. Blood quills formed ≥25% (ASY Black Brant) to ≥50% (SY Black Brant) of back and rump, breast, and side regions during remex regrowth. Maximum molt intensity, as estimated by the number of blood quills, occurred when primaries were about 50% grown (20-22 July). Still, Black Brant completed growth of only 11 to 21% (TPN 12-21) of all feathers prior to leaving the molting area. SY Black Brant replaced more body feathers than did ASY Black Brant during the flightless period. Failed-nesting Black Brant, like Canada Geese (Gates et al. 1993), seem to postpone replacing most body feathers until after completing remigial molt. My study supports the hypothesis by Gates et al. (1993) that postbreeding geese may concentrate energy and nutrients on remex growth (in lieu of an extensive body molt), which in turn may allow a shortening of the flightless period. Molt intensity generally did not differ between males and females within age classes, concurring with Gates et al. (1993).

A partial rectrix molt occurred before and during wing molt. SY Black Brant rectrix molt frequency and intensity exceeded that of ASY Black Brant, supporting the hypothesis of protein and lipid conservation by postbreeding adults (Gates et al. 1993). The average number of rectrices was 16 (Cramp and Simmons 1977, my study); however, the number of feathers present ranged from 10 to 18. Although rectrices were not shed simultaneously (see also Weller 1957, Oring 1968, Young and Boag 1981), two to seven tail feathers were replaced concurrently in a symmetrical pattern.

Distal primaries (nos. 6-10) dropped prior to those more proximal. The tenth primary emerged first and exceeded the ninth primary in length until the latter reached approximately 15% (≈34 mm) of its final length. The shorter proximal primaries matured before longer distal remiges, as previously reported in Redheads (*Aythya americana*; Weller 1957), Mallards (*Anas platyrhynchos*; Young and Boag 1981), and Lesser Scaups (*Aythya affinis*; Austin and Fredrickson 1986).

Outer primary, secondary, and lesser wing coverts are replaced prior to their innerwing counterparts, which likely decreases thermoregulatory cost (Payne 1972) because exposure of vascularized feather papillae occurs on only one wing surface at a time. Black Brant are similar to Redheads (Weller 1957) and Mallards (Young and Boag 1981) in molting outer middle and inner primary coverts at a slower rate and over a longer period compared with other coverts.

Comparison of remigial growth rates among species of waterfowl is confounded because previous studies often failed to record feather type and position (Hohman et al. 1992). Furthermore, because growth rates of individual feathers are not constant, the range over which measurements are recorded is critical if comparisons between species and habitats are to have meaning. Realizing these limitations, the ninth-primary growth rate (7.2 mm/day) derived for Black Brant at Teshekpuk Lake is similar to mean values previously reported for Canada Geese (7.3 mm/day; Hanson and Jones 1976) and Barnacle Geese (*Branta leucopsis*; 7.5 mm/day; Owen and Ogilvie 1979), but higher than the 5.9 mm/day rate measured for nine Brent Geese (*Branta bernicla*) in the Queen Elizabeth Islands (Boyd and Maltby 1980).

Primary growth rates of Black Brant (my study), Barnacle Geese (Owen and Ogilvie 1979), and Canada Geese (Gates et al. 1993) did not differ between ages and sexes. Primary growth rate in Black Brant declined in relation to remex emergence, supporting previous observations on Canada Geese (Hanson 1965), but contrasting with the uniform rate observed for Barnacle Geese (Owen and Ogilvie 1979). Changes in feather-growth rate over the flightless period may be obscured because: (1) growth-rate estimates often are obtained only during early and midmolt as geese usually attain flight before feather maturation; and (2) growth rates based on feathers that have not emerged are likely to be underestimated due to the lag time before visible growth occurs (see Owen and Ogilvie 1979, Boyd and Maltby 1980, Geldenhuys 1983, Panek and Majewski 1990). In my study, the mean primary growth rate determined from initial primary lengths of 0 mm (i.e. primary feather had not emerged) was significantly slower than that derived from primaries that had emerged (6.3 vs. 7.3 mm/day, respectively).

The nonsignificant relationship between primary growth rate and Julian date in my study probably reflects the range of molt initiation (26 June–25 July). Primary growth rate also was not correlated with body mass, although body mass (Taylor 1993) and primary growth rate declined in relation to ninth-primary length. Owen and King (1979) reported that Mallard body mass and early growth rates were positively correlated; however, a later study (Panek and Majewski 1990) found no such relationship.

Migration and molt chronology may be directly related to season phenology and ice breakup (Sterling and Dzubin 1967). Brant began molt three to five days earlier in 1988 when the mean daily temperature in June was 2°C warmer than in 1989 (Taylor 1993:table 0.2). Thus, the availability of open water may have been greater in 1988, allowing earlier molt. However, molt chronology of Brant measured on two lakes differing in ice break-up and open water availability were not different. Early arriving Black Brant select shallow, turbid lakes that become ice-free before deeper lakes (Derksen et al. 1979). Prior to becoming flightless, geese may shift to deeper lakes with ice cakes, that are used for preening, resting, and escape sites (Derksen et al. 1979).

Failed nesters and nonbreeders arrived in the Teshekpuk Lake molting area primarily from late June through mid-July (Derksen et al. 1979, 1982, my study). Remigial molt started during the first week in July (Derksen et al. 1979, my study), although some failed nesters arrived and began molt from mid- to late July. At Teshekpuk Lake, molting-chronology estimates must take into consideration: (1) birds initiate molt over a one-month period; (2) variability in the arrival of SY, ASY, and nonbreeding versus failed-nesting Black Brant; and (3) differences in available molting habitat (open water) between shallow and deep lakes. Furthermore, this molting population is comprised of individuals from breeding colonies in Alaska, Canada, and Russia. Differences in reproductive effort and migration likely influence body condition, which then ultimately may affect the chronology, pattern, and intensity of molt (see Gates et al. 1993).

Environmental and hormonal cues (Greij 1973) may further affect the feather-replacement chronology within and among age, sex, and breeding classes. Molt chronology and regrowth appear similar between ASY and SY Black Brant for birds initiating molt in early to mid-July. The significantly longer mean ninth primary of nonbrood-patch ASY females than brood-patch ASY females for most samples after 17 July was likely the result of a late migration of brood-patch ASY females from breeding colonies along the Yukon-Kuskokwim Delta, or perhaps Russia. Subadult and nonbreeding adult Barnacle Geese also did not differ in molt chronology, but breeding adults (males and females) began molt 9 to 10 days later than nonbreeders (Owen and Ogilvie 1979). As with Barnacle Geese, synchrony of molt was greatest among SY Black Brant, followed by nonbrood-patch ASY females, while brood-patch ASY females were most variable.

Black Brant are capable of sustained flight when the ninth primary is about 70% grown; however, some birds flew when the ninth primary averaged 62% of its final length. Boyd and Maltby (1981) reported brant could fly when primaries reached 65% of final length, and Ankney (1984) estimated primaries must be greater than 75% of definitive length. Whereas it is possible that Black Brant in this study were capable of flight at primary lengths shorter than those recorded, handling stress, wind-aided flight, and below-average body mass probably induced early flight capability. Indeed, the mean fresh body mass of Black Brant observed to fly was 24 to 89 g lower than the mean mass for the overall late-molt population. This supports earlier studies reporting that molters with the lowest body masses are the first birds capable of flight (Owen and Ogilvie 1979, Geldenhuys 1983).

Assuming that (1) primaries require two days to emerge after being dropped, (2) primary growth rate equals 7.2 mm/day and then declines, and (3) sustained flight occurs when the ninth primary has completed 70% of its growth, the duration of the flightless period is about 23 and 24 days for females and males, respectively, supporting an earlier estimate by Derksen et al. (1979) of 3 to 3.5 weeks. Previous studies report similar findings for brant (about 21 days, Palmer 1976; 22-25 days, Boyd and Maltby 1980), Barnacle Geese (25 days, Owen and Ogilvie 1979), Canada Geese (25 days, Sterling and Dzubin 1967), and Greylag Geese (*Anser anser*; 28 days, Loonen et al. 1991).

Management implications.—The timing and duration of flightlessness, and the relationship between molt and nutrient (lipid and protein) reserves, are critical in determining the time frame and potential impacts of petroleum exploration. In 3.5 weeks, Black Brant molt and regrow (to 70% maturity) all of their remiges in addition to renewing at least 25% of the back, rump, breast, and side regions. Concurrently, lipid reserves decline 71 to 88% and comprise only 2 to 4% of corrected fresh body mass during late molt (Taylor 1993). Although Arctic-nesting geese benefit from rapid feather growth and early regaining of flight (as result of mass loss; Taylor 1993), these benefits are lost if environmental perturbations and disturbance preclude uninterrupted feeding to allow feather maturation.

Flightless Black Brant are present in the Teshekpuk Lake molting area from 26 June through 19 August although pre- and postmolters extend both of these dates by several weeks. My study supports earlier recommendations (King 1970, Derksen et al. 1979, 1982) that the Teshekpuk Lake molting area should be protected from petroleum exploration during the entire period Black Brant are present.

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