MOLT IN THE ANNUAL CYCLE OF CANVASBACKS

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ABSTRACT.—We studied the intensity of molt of capital, down, and contour plumages of male and female Canvasbacks (*Aythya valisineria*) from late fall through winter, spring migration, and nesting. Molt intensities in both juvenile and adult males were highest among arriving fall migrants and during prewinter fat deposition, and molt in juvenile males increased during early spring migration. Among females, capital molt was high among arriving migrants in fall, and molt of all plumage types increased during spring migration and courtship. Paired females tended to molt more heavily than unpaired females during spring migration, but many females initiated intensive prebasic molt before pairing. Molt in females peaked in spring migration and early breeding, concurrently with accelerated fat storage and ovarian growth. Capital and contour molt in females decreased during laying and essentially ceased during incubation, perhaps to mitigate energetic constraints during these periods. Prewinter nutrient storage appeared independent of molt intensity, except for body protein among juveniles. During spring migration, molt intensities were greater in adult females with higher levels of body fat and protein, indicating that molt did not necessarily precede or interfere with nutrient storage. We suggest that outside the laying, incubation, and wing molt periods, the energetic costs of molt in Canvasbacks are not sufficient to mandate temporal separation of molt from nutrient storage, migration, courtship, or early stages of rapid ovarian growth. *Received 14 September 1987; accepted 29 March 1988.*

THE costs of avian molt include nutrient demands for feather components, increased amino acid metabolism, changes in water balance, increases in blood volume, and enhanced heat loss (King 1980). These and other adjustments logically seem to require changes in a bird's allocation of time and energy. However, the energetic and nutritional costs of molt have proven difficult to partition from those of other physiological or ecological processes (Payne 1972, King 1980, Walsberg 1983, Ankney 1984), so that inference as to the energetic significance of molt has been largely theoretical rather than empirical (e.g. Walsberg 1983, Heitmeyer 1985: 289–298). Consequently, despite recent insights into molt physiology (e.g. Murphy and King 1984, 1986), there is disagreement over whether the energy demands of molt constrain other events in the annual cycle (Payne 1972, Walsberg 1983).

That annual cycles of birds have evolved to minimize overlap of energetically demanding events has been repeatedly asserted (Payne 1972, King 1974, Wingfield and Farner 1980, Heitmeyer 1987). This "staggered costs" hypothesis has in some cases been extended to a "sequential events" hypothesis, by which the initiation of presumably expensive events such as molt, nutrient storage, migration, courtship, and breeding is contingent on completion of preceding events (Heitmeyer 1985: 153; see Farner et al. 1980). These ideas imply that overlap of such processes would at times be prohibitively stressful (King and Murphy 1985). Perhaps because the costs of molt are so uncertain (Payne 1972, Walsberg 1983), workers have often speculated that seasonal molt patterns reflect a staggered costs strategy (Payne 1972; Owen and Krohn 1973; Chilgren 1977; Heitmeyer 1985, 1987; Miller 1986), despite many examples of molt coinciding with other demanding processes (Erskine 1971, Billard and Humphrey 1972, Payne 1972, Foster 1974, Page 1974, Young and Boag 1982, Paulus 1984, DuBowy 1985, Wishart 1985, Austin and Fredrickson 1986, Gruenhagen 1987).

The energetic significance of molt is also at issue in its use as an indicator of the physiological status, habitat requirements, and probable fitness of migrants in nonbreeding birds. For example, in winters of low habitat availability molt is delayed in Mallards (*Anas platyrhynchos*) and Northern Pintails (*Anas acuta*) (Heitmeyer 1987, Miller 1986). Shortage of food,

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or perhaps of particular food types (Petersen 1981), may hinder timely completion of molt. This also implies that individuals more capable of acquiring resources may exhibit advanced molt chronology, so that analyses of patterns of nutrient reserves might be improved by including molt status as a covariate (Heitmeyer 1985).

The value of molt descriptions in such analyses hinges on whether there are important consequences to retarded molt. Possible disadvantages include delays in nutrient storage, pairing, or migration (Paulus 1984, Heitmeyer 1985, Wishart 1985, Miller 1986), in which molt supposedly slows the progress of sequential events, or forces birds to incur otherwise staggered costs simultaneously. Hence, the energetic significance of molt in the annual cycle should be reflected in the degree to which overlap of molt with other costly events is avoided.

We describe the intensity of molt of capital, down, and contour plumages in free-ranging Canvasbacks (*Aythya valisineria*) throughout winter, spring migration, and breeding. We use these data to examine the applicability of the staggered costs concept to molt in Canvasbacks.

STUDY AREAS AND METHODS

Canvasbacks were collected by shooting at major concentration areas from late fall through winter, spring migration, and nesting (Table 1; see Bellrose 1980). Canvasbacks begin arriving at Lake Mattamuskeet, North Carolina, during the first week of November, and move from the lake to Pamlico Sound during the first 2 weeks of December. Northward movement begins in late February, and migrants apparently stage in upper Chesapeake Bay until open water allows further migration. Canvasbacks then migrate west across the Great Lakes region to the upper Mississippi River near La Crosse, Wisconsin, where they mix with Canvasbacks migrating north from wintering areas along the Gulf Coast and Mississippi valley. They then move to nesting areas located primarily in the pothole region of North Dakota and the Canadian prairies.

Pair status in spring was determined by a combination of spatial proximity, inciting by the female, mutual neck-stretching, copulation, and selective threats and chases by pair members (display descriptions in Palmer 1976).

We plucked rectrices, remiges, scapulars, tertials, and wing coverts by hand and examined them for blood quills that indicate active growth. Remaining feathers were cut off near the base with sheep shears or dog clippers. Molt was recorded for different body regions (Billard and Humphrey 1972: fig. 3), and down feathers in the spinal, side, and leg apteria were also scored. Blood follicles in the capital (head and neck) region were counted from underneath the skin after removal of fat and bloody fascia. Contour and down feathers were not distinguished in the capital region. Blood follicles on the rest of the body were counted from the outside surface of the skin. Follicles of contour feathers were characterized by rigid quills at the base, their large size, and their occurrence within orderly lines of follicles. Incoming down feathers were small, dark, lacked basal quills, and occurred outside of follicle lines.

We used total counts of blood follicles, and classes of total blood-follicle counts based on percentages of the maximum observed numbers of incoming feathers. These classes were defined as <5%, 5-20%, 20-50%, and >50% of the following observed maxima of blood follicles: capital 2,240, contour 980, and down 2,420. Thus each duck had 3 scores that corresponded to capital, contour, and down plumages. Counts for these plumages were for 1 side of the body only. We did not assign qualitative molt-intensity scores for different tracts and sum these scores to compute an overall score for each bird (e.g. Billard and Humphrey 1972, Bailey 1981, Young and Boag 1981). The latter method does not take into account the substantial variation in total numbers of follicles in each tract. (For 4 male and 4 female Canvasbacks collected February-May, the total contour follicles on 1 side of the body in Billard and Humphrey's tracts II-VI were [$\bar{x}$ ± SD] 286 ± 59, 298 ± 57, 749 ± 100, 250 ± 43, and 70 ± 17, respectively.) Qualitative molt scores also do not allow direct comparisons of data between studies, because the relative intensity classes represent different numbers of incoming feathers depending on the range of molt intensity within a particular sex or study period.

Samples of breeding Canvasbacks from the Erickson and Minnedosa sites in southwestern Manitoba (see Table 1) were combined by sex, with the breeding stage of females and their mates classified according to the female's ovarian development. Females with largest ovum diameter ≥7.45 mm were categorized as being in rapid ovarian growth (ROG). This size criterion was based on an associated change in ovum color from gray to yellow (see Romanoff and Romanoff 1949). Largest ovum diameters of females in ROG fell naturally into 2 size groups, which we classified as early ROG (7.81-18.01 mm) and late ROG (22.26-37.45 mm). This division corresponded to the midpoint of ROG, given that the largest ovum diameter of 13 laying females with developing follicles averaged 38.26 ± 4.07 (SD) mm. We defined all Canvasbacks hatched the preceding summer as juveniles, even though many females breed in their first year (see Anderson 1985).

Sheared carcasses were homogenized in a meat grinder, and subsampled for determination of ash and

TABLE 1. Localities and dates of collection for Canvasbacks used in molt analyses.

- Lake Mattamuskeet, North Carolina
  - 3-17 November 1982 and 1983
  - 21 November-2 December 1982 and 1983
- Pamlico Sound, North Carolina
  - 14-16 December 1983
  - 12-30 January 1984
  - 6-19 February 1983 and 1984
- Mississippi River near Keokuk, Iowa
  - 25 February-17 March 1984
- Long Point Bay, Lake Erie, Ontario
  - 7 March-10 April 1984
- Mississippi River near La Crosse, Wisconsin
  - 24-30 March 1984
- Woodworth and Valley City areas, North Dakota
  - 7-18 April 1984 and 1985
- Erickson, Manitoba
  - ROG[a]: 24 April-3 May 1984
- Minnedosa, Manitoba (1977-1981)
  - ROG: 24 April-1 June
  - Laying: 7-28 May
  - Incubation: 10 May-9 July
  - ROG renest: 12 May-4 June

[a] Rapid ovarian growth.

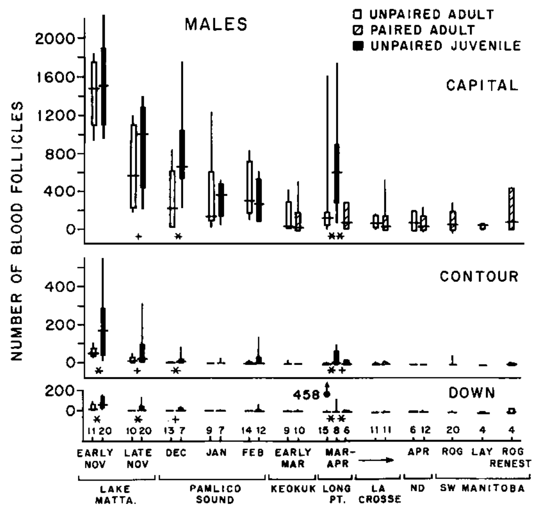

Fig. 1. Molt intensities for capital, contour, and down plumages of male Canvasbacks. Horizontal lines are medians, bars are 15-85% quantiles, and vertical lines are ranges. Sample sizes are on bottom abscissa. Differences between adjacent samples (Wilcoxon rank sum tests) are indicated by asterisks for 0.05 level and pluses for 0.10 level.

lipid content (soxhlet extraction in ethyl ether or Randall extraction in petroleum ether). Body protein was estimated by ash-free lean dry mass (Lovvorn 1987). Previous removal of internal organs from some of the Canvasbacks in our breeding sample reduced sample sizes for some analyses involving body protein.

We used the Statistical Analysis System (SAS Institute, Cary, North Carolina) for all analyses. Differences at the 0.05 level were considered significant unless otherwise stated. For regressions, we log-transformed blood-follicle counts to stabilize variances and improve linearity. In regressions involving categories such as breeding stage, we used binary indicator variables (Neter and Wasserman 1974: 297-312). For stepwise regressions we used the SAS STEPWISE procedure, which includes elements of both forward and backward stepwise methods.

RESULTS

Differences between years.—Except for breeding ground samples, most Canvasbacks were collected in the fall, winter, and spring of 1983-1984 (Table 1). Sample sizes in the preceding or subsequent years were small, and we tested for differences in blood-follicle counts between years only in cases where the smaller sample size was ≥ 4. None of these tests were significant (t-tests, $P > 0.05$), so data from different years were pooled. Samples from the Minnedosa breeding area were too small to test for between-year differences and data from 1977-1981 were combined.

Males.—Juvenile males in general molted more intensively than adult males from November-January and in early spring migration (Figs. 1, 2). Adults completed prealternate molt of contour and down plumages in fall, but molt into Prealternate I by juveniles resumed after the midwinter low in molt activity (see Palmer 1976: 137-142 for feather-generation terminology). Molt of body plumage was negligible in adult males throughout winter, spring migration, and breeding, regardless of pair status. In both adults and juveniles, capital molt was variable but continued throughout the study period. Molt of tertials and rectrices was virtually complete by January, but molt of scapulars continued throughout winter and increased again in February, especially in juveniles. In general, molt intensities in both juvenile and adult males were highest among arriving migrants in fall and during prewinter fat deposition (Lovvorn 1987).

Females.—Molt in females was less intense than in males upon arrival in North Carolina (Figs. 3, 4). In February and March, feather re-

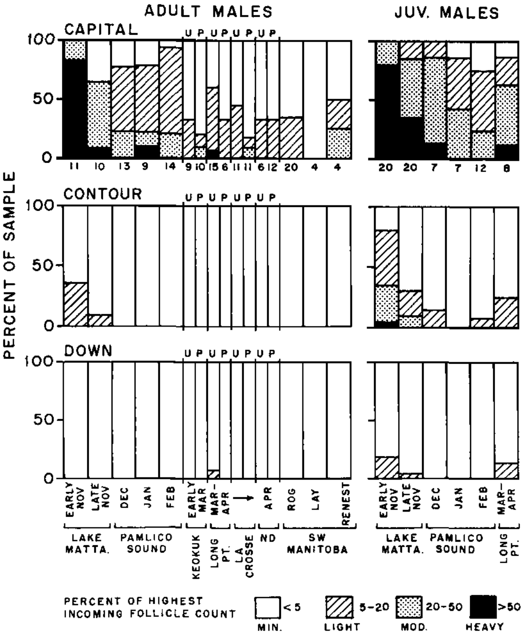

Fig. 2. Percentages of male Canvasbacks in different molt-intensity classes. Sample sizes are noted underneath the top figure. U = unpaired, P = paired.

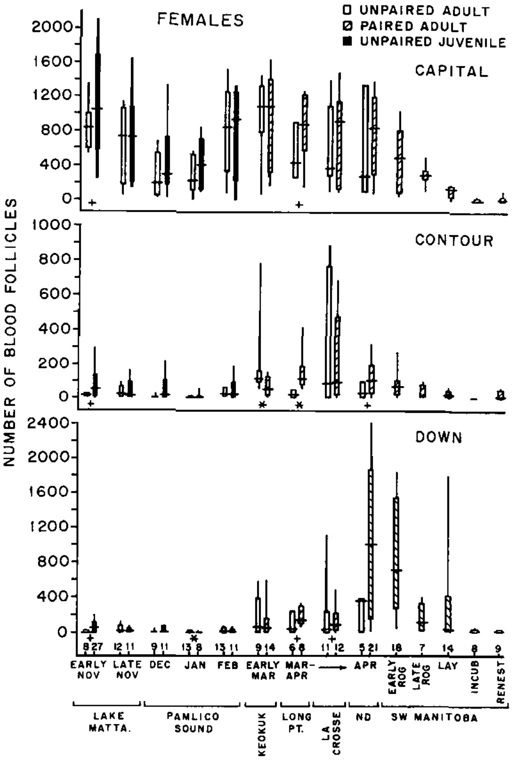

Fig. 3. Molt intensities for capital, contour, and down plumages of female Canvasbacks. Conventions as in Fig. 1.

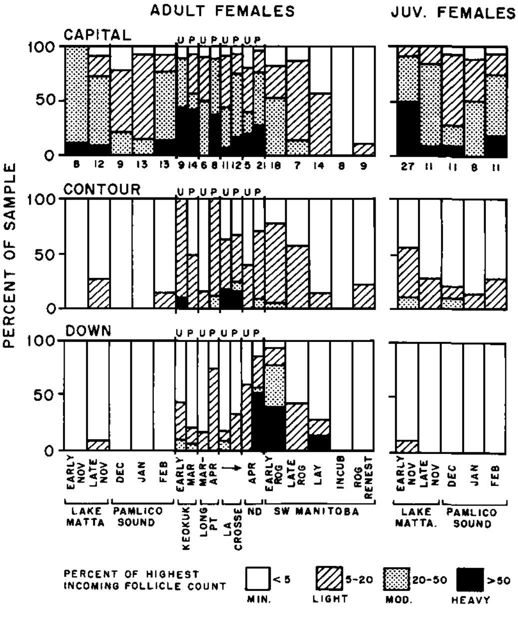

Fig. 4. Percentages of female Canvasbacks in different molt-intensity classes. Conventions as in Fig. 2.

placement in females increased dramatically with onset of prebasic molt. Although differences were not always significant, prebasic molt was greater in paired than unpaired females during spring migration at Long Point, La Crosse, and North Dakota. An intensive prebasic molt before pairing in females was especially evident in early March at Keokuk, where contour molt was greater in unpaired than in paired females.

In females, down and contour molt virtually stopped and capital molt was reduced in midwinter. Replacement of tertials, scapulars, and rectrices continued from November through rapid ovarian growth, with a peak in scapular molt from February through April. In general, molt intensity was high among arriving fall migrants, during spring migration and courtship, and after arrival on breeding areas. Capital and down molt peaked in late spring migration and early breeding, concurrently with accelerated storage of fat for nesting and with growth of ovarian follicles (J. A. Barzen unpubl.; Barzen and J. R. Serie MS). Contour molt peaked in mid-migration and also continued into the period of rapid ovarian growth. Capital and contour molt decreased during laying, and essentially ceased during incubation.

TABLE 2. Stepwise linear regressions of molt intensities (log of blood-follicle counts) of migrating adult female Canvasbacks vs. date, body fat, body protein, pair status, and all two-way interactions. All variables retained in stepwise models with $P \leq 0.10$ are reported. Signs before r^2 values indicate direction of relationship. Simple coefficients of determination are also given for component terms of significant interactions.

Location	n	Plumage	Variable[a]	Simple r^2	Partial r^2	P[b]
Keokuk	23	Contour	Status	−0.29	−0.29[c]	<0.01
Long Point	14	Contour	Status × protein	0.65	0.65	<0.01
			Status	0.62		<0.01
			Protein	<0.01		0.95
		Down	Status	0.35	0.35	0.02
La Crosse	23	Capital	Protein × date	0.22	0.22	0.02
			Protein	0.15		0.07
			Date	0.05		0.30
		Contour	Protein × date	0.31	0.31	<0.01
			Protein	0.24		0.02
			Date	0.07		0.22
		Down	Protein × date	0.41	0.41	<0.01
			Protein	0.28		<0.01
			Date	0.07		0.22
North Dakota	27	Capital	Fat × status	0.14	0.14	0.05
			Fat	0.11		0.08
			Status	0.02		0.48
		Contour	Fat	0.15	0.15	0.04
		Down	Protein × date	0.24	0.24	<0.01
			Protein	0.22		0.01
			Date	0.02		0.53
All sites	86	Capital	Fat × status	0.04	0.04	0.06
			Fat	0.02		0.18
			Status	0.01		0.29
		Contour	Protein	0.04	0.04	0.06
		Down	North Dakota × fat	0.26	0.26	<0.01
			North Dakota	0.18		<0.01
			Fat	0.06		0.02
			Protein	0.16	0.05	0.01
			Long Point × status	<0.01	0.03	0.05
			Long Point	<0.01		0.62
			Status	<0.01		0.73

[a] Listed in order of inclusion in stepwise model for a given location and plumage.

[b] For variables included in stepwise models, P-value is partial significance of inclusion rather than significance of simple r^2.

[c] Partial r^2 for inclusion in stepwise model.

Molt intensity, date, and prewinter nutrient storage.—We analyzed molt intensities relative to date, body fat, and body protein for adult and juvenile males and females in early and late November, and for both periods combined. Molt intensity was not related to date for any sex-age class within sampling period; but when data from early and late November were combined, molts of all plumages were negatively correlated with date for adult and juvenile males ($P < 0.01$; r^2 for different plumages ranged from 0.52–0.62 for 21 adults, 0.24–0.29 for 40 juveniles). Among females, date was related (negatively) only to capital molt in adults ($r^2 = 0.22$, $P = 0.04$, $n = 20$), with no significant correlations between date and molt in juveniles ($n = 38$). The difference between juvenile males and females in association of molt with date apparently reflected delayed completion of postjuvenile molt until spring by females. No relationships between molt intensity and body fat were apparent. The same was true for body protein, except that in early November, juveniles with lower body protein had lower intensities of capital and down, but not contour, molt (for 20 juvenile males: capital $r^2 = 0.54$, down $r^2 = 0.39$; for 27 juvenile females: capital $r^2 = 0.31$, down $r^2 = 0.22$; $P < 0.01$). Such effects were no longer apparent by late November.

To investigate the relationships among molt,

TABLE 3. Results of stepwise linear regression of molt intensities (log of blood-follicle counts) of adult female Canvasbacks vs. date, breeding stage, body fat, body protein, and all two-way interactions. Stages 1-5 were, respectively, early ROG (rapid ovarian growth) ($n = 15$), late ROG ($n = 5$), laying ($n = 13$), incubation ($n = 8$), and ROG for renesting ($n = 8$). All correlations with $P < 0.10$ are reported. Signs before r^2 values indicate direction of relationship.

Plumage	Variable[a]	Partial r^2	P[b]
Capital	Date	−0.51	<0.01
	Stage 5	−0.12	<0.01
Contour	Date	−0.58	<0.01
	Protein × stage 5	−0.08	<0.01
	Fat × stage 4	−0.07	<0.01
Down	Stage 1	0.44	<0.01
	Date × stage 5	−0.11	<0.01
	Protein × stage 4	−0.12	<0.01
	Stage 4	0.03	0.03

[a] Listed in order of inclusion in stepwise model.

[b] Partial significance (F-test) of inclusion in stepwise model.

date, and nutrient storage in adult females during spring migration, we analyzed molt intensities vs. date, body fat, body protein, pair status, and all two-way interactions for Keokuk, Long Point, La Crosse, North Dakota, and all sites combined (Table 2). Early in migration at Keokuk and Long Point, molt was largely independent of body composition and was associated primarily with pair status. However, trends with pair status were reversed for the 2 areas. At La Crosse, molt was more intense among females with higher body protein, this tendency increasing with advancing date. In North Dakota, where at least some females were close to their breeding areas, fat became the most important correlate of molt intensity; molt was also higher in paired females and in those with greater body protein. Date was not a significant variable in a stepwise regression involving the entire migration sample (Table 2).

TABLE 4. Results of stepwise linear regressions of molt intensities (log of blood-follicle counts) vs. date, largest ovum diameter, body fat, body protein, and all two-way interactions for combined early and late periods of rapid ovary growth in adult female Canvasbacks ($n = 20$). Signs before r^2 values indicate direction of relationship.

Plumage	Variable[a]	Partial r^2	P[b]
Capital	Date × protein	−0.21	0.04
Contour	Date	−0.21	0.04
Down	Date	−0.43	<0.01
	Ovum diameter × fat	−0.12	0.05

[a] Listed in order of inclusion in stepwise model.

[b] Partial significance (F-test) of inclusion in stepwise model.

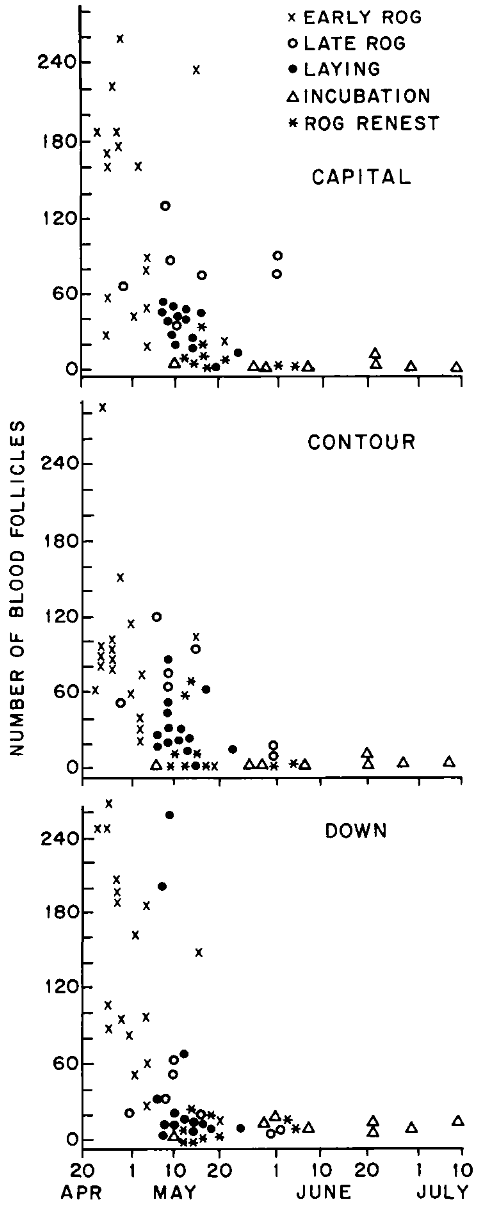

Fig. 5. Molt intensities of adult female Canvasbacks during early ROG (rapid ovarian growth), late ROG, laying, incubation, and ROG for renesting in southwestern Manitoba, 1977-1984.

Relative importance of date, breeding stage, and nutrient status.—In breeding females, the relative association of molt intensity with date was complex and varied among plumages (Fig. 5, Table 3). Stepwise regressions suggested that Julian date was far more important than breeding stage or nutrient status as a correlate of both capital and contour molts. When early and late ROG (rapid ovarian growth) were combined (Table 4), date had the highest coefficient of determination for all plumages, including down. Down molt also decreased independently of date with increasing fat and ovum size. Over all breeding stages (Table 3), associations of molt with nutrient status were evident only during incubation and renesting, when molt intensity was higher in birds with lower fat and protein reserves.

Molt was varied, and often intense during ROG and laying. Molt was more closely associated with date (phenology, photoperiod) than with reproductive chronology. However, molt fell to negligible levels during late laying and incubation, when associations of molt with nutrient status became apparent. Samples of breeding juvenile females were too small for analyses, but their molt patterns resembled those of adults.

DISCUSSION

Nutrient storage and stage of molt completion.—We did not collect data on stage of completion of prealternate or prebasic molts. Stage of molt completion might provide information on the recent history of molt costs in individuals, and would aid in interpreting relationships between molt intensity and levels of stored nutrients. However, molts of different feather generations are often slowed or interrupted (Palmer 1972), so that inference as to recent molt costs may be unreliable. We attempted to test the mechanistic basis for the staggered costs or sequential events hypotheses relative to molt, i.e. that the energetic demands of molt are such that temporal overlap of molt with costly events is avoided. Molt intensity, rather than state of completion, seemed the more appropriate measure for our purposes.

Nutrient storage by female Mallards may be reduced until after completion of prebasic molt in spring or of prealternate molt in fall (Heitmeyer 1985: 193, 198). In female Canvasbacks, peak fat levels (J. A. Barzen unpubl.) were reached before or concurrently with peaks in prebasic molt during late spring migration (Figs. 3, 4). Furthermore, during prealternate molt in November, body fat was independent of molt intensity in all sex and age classes. The same was true of body protein, except for early fall juveniles whose patterns of body protein and molt were probably functions of growth since hatching. During spring migration, molt intensities were greater in adult females with higher levels of body fat and protein (Table 2). This suggests that molt did not necessarily precede or interfere with nutrient storage. Among breeding adult females, correlations of molt intensity with nutrient status were minimal, and in general only apparent during laying, incubation, and renesting when little molt occurred (Table 3). Moreover, correlations between molt and body composition could merely reflect covariation of independent processes with time, ontogeny, pair status, or individual photoperiodic response, so that no causal relationships between molt and nutrient levels necessarily exist. We believe that if there is a relationship between stage of molt completion and nutrient deposition in Canvasbacks, it is probably not energetically based.

Pairing and prebasic molt in females.—Prebasic molt was generally more intense among paired than unpaired female Canvasbacks during migration (Figs. 3, 4). However, in Canvasbacks, prebasic molt did not occur only after pairing as suggested for Mallards (Heitmeyer 1985: 153). Many Canvasback females molted heavily during migration before forming pair bonds. Molt intensities among recently paired female Canvasbacks cannot be explained in terms of enhanced female foraging efficiency owing to mate defense by the male, because male Canvasbacks do not defend females at that stage in the breeding sequence (Lovvorn 1987). Furthermore, data on Canvasbacks (J. A. Barzen unpubl.; Lovvorn 1987, this study) do not support the hypotheses that initiation of either pairing or prebasic molt by females are generally constrained by body condition (Heitmeyer 1985: 194, 197).

It is unclear why there was a detectable tendency for paired female Canvasbacks to molt more heavily at a given time than unpaired females (Figs. 3, 4). Reversal of this trend at Keokuk suggests that the statistical differences we found may be spurious. However, the average physiological state of birds migrating through an area can vary with timing relative to the peak of migration (Rappole and Warner 1976, LaGrange 1985). We collected most Canvasbacks during periods of highest numbers at the migration sites. Nevertheless, it is possible that individuals in different physiological states remained longer in certain areas, so that different subpopulations were sampled disproportionately depending on the sampling times.

Photoperiod-endocrine relationships in migrants might be altered by individual variation in breeding latitude. Canvasbacks nest from Minnesota to northeastern Alaska (Bellrose 1980). This wide range of breeding latitudes could correspond to appreciable differences in pairing, molt, and nutrient storage chronologies through varied rates of photoperiodic response (Williamson and Emison 1971). The unpaired females at Long Point, La Crosse, and North Dakota with less intense prebasic molt might simply have had farther to migrate before nesting than paired females collected in the same areas.

Relative importance of date, breeding stage, and nutrient status.—The energetic significance of molt patterns during breeding depends on the nutrient and energy demands of molt and egg production, relative to foraging efficiency (perhaps for specific nutrients) and foraging time available. Because stored reserves measure nutrient and energy balances, it appears that molt intensity during the breeding period is more a function of date than of proximate availability of exogenous energy or nutrients (Tables 3, 4). The costs of synthesizing reproductive tissue during laying are uniformly high relative to such costs during rapid ovarian growth (e.g. Drobney 1980). The patterns of molt intensity during these two periods may reflect adaptation to avoid overlap of molt with egg production. Similarly, low molt intensity during incubation might correspond to restricted feeding time (Anderson 1985). Nevertheless, levels of contour and down molt during laying were as high or higher than during fall and winter (Figs. 3, 4), suggesting that the costs of molt in female Canvasbacks are not great enough to conflict with prenesting activities.

Molt as an influence on annual cycles.—Avoiding overlap of the energetic costs of molt with migration, nutrient storage, courtship, and breeding is cited as an important adaptive strategy in the annual cycles of ducks (e.g. Heitmeyer 1985, 1987; Miller 1986). The data for Canvasbacks outside the laying, incubation, and wing molt periods are inconsistent with this reasoning. In males, molt intensities were highest in arriving fall migrants and during prewinter fat deposition, and molt in juveniles increased during spring migration. Molt in females peaked in spring migration and early breeding, concurrently with accelerated storage of fat for nesting and with rapid ovarian growth (J. A. Barzen and J. R. Serie MS). We believe that interpreting annual molt patterns as strategies to avoid overlap of molt with migration, nutrient storage, courtship, or breeding is an approach of limited generality. This view is supported by data on other species of ducks, in which there is substantial overlap of molt with these events (Erskine 1971, Billard and Humphrey 1972, Palmer 1976, Young and Boag 1982, Paulus 1984, DuBowy 1985, LaGrange 1985, Wishart 1985, Austin and Fredrickson 1986, Gruenhagen 1987).

We do not claim that molt is not costly. Although estimates vary widely and the mechanisms are unclear, molt is reported to increase basal metabolism by 9–46% (Walsberg 1983). Furthermore, stability or increase of body nutrients during molt do not preclude nutrient deficits (see discussion in Bailey 1985). Molt will influence the timing of other events only if birds are unable to meet the costs of molt simultaneously with other demands (King and Murphy 1985). In this context, we define "stress" as a situation when demands of one event (physiological, behavioral, or otherwise) are great enough to interfere with desirable allocation of resources to other processes. By this definition, no matter how demanding a process is, if it does not reduce necessary allocation to other purposes, it is not considered stressful. Similar arguments have been advanced (Ankney 1979, 1984; DuBowy 1985; Austin and Fredrickson 1987) relative to the postbreeding molt period.

Evidence for stress of molt in wild ducks has been entirely correlative (Heitmeyer 1985, 1987; Miller 1986). For example, based on clear differences in molt patterns between wet and dry winters in California, Miller (1986) suggested that poor habitat conditions caused a delay in prebasic molt by female Northern Pintails. Altered habitat conditions can produce major changes in bird distributions (Nichols et al, 1983, Terrill and Ohmart 1984) and in population composition (e.g. latitude of breeding origin, age, body size) of birds present in a given year (Gordon 1981, Terrill and Ohmart 1984). Such shifts might be accompanied by changes in local molt patterns that are innate rather than direct consequences of food intake.

In the breeding season, prebasic molt in male

Canvasbacks and Redheads (*Aythya americana*) begins earlier in nonbreeders and failed breeders than in successful pairs (Hochbaum 1944, Bailey 1981; see also Austin and Fredrickson 1986). Within the appropriate range of photoperiod (Farner et al. 1980, Wingfield and Farner 1980), the costs of reproduction in ducks appear to influence when prebasic molt begins (males) or resumes (females). However, the situation in Canvasbacks signals caution in interpreting molt patterns of ducks in terms of staggered costs or sequential events.

Molt status as an indicator of fitness.—In Gadwalls (*Anas strepera;* Paulus 1984) and American Wigeon (*A. americana;* Wishart 1985) individual males that complete prealternate molt sooner tend to pair earlier. Early pairing in dabbling ducks is assumed to confer (or reflect) superior access to food (e.g. Paulus 1983, Hepp 1984, Heitmeyer 1985). Because molt intensity, pairing chronology, and nutrient stores probably covary with the photoperiodic responses of different individuals, it is difficult to distinguish cause and effect among these variables in wild populations.

In some cases, relative proficiency at acquiring resources may be secondary to photoperiodic response in dictating individual variation in molt chronology (see Tables 3, 4). Manipulated photoperiods altered rates of prealternate molt and testes enlargement in adult and juvenile male Mallards (Storey and Nicholls 1978). Bailey (1981) reported that initiation of prebasic molt in male Redheads was advanced in a year when breeding was terminated early. However, the consistent annual timing and intensity of prealternate molt in male Redheads seemed unaffected by events in the breeding season or by timing of prebasic molt, suggesting strong photoperiodic influence.

Molt chronology is probably a function of both photoperiodic controls and proximate resource or behavioral cues (Wingfield and Farner 1980). Outside the laying, incubation, and wing molt periods, energetic constraints on molt in Canvasbacks appear insufficient to mandate temporal separation of molt from other energetically expensive events in the annual cycle.

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