DEFINITIVE PREBASIC MOLT OF GRAY CATBIRDS AT TWO SITES IN NEW ENGLAND[1]

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Abstract. We studied the pattern and timing of prebasic molt in adult Gray Catbirds (*Dumetella carolinensis*) at two New England sites: Block Island, Rhode Island (BIRI), and the Vermont Institute of Natural Science (VINS) in Woodstock, Vermont. Catbirds at VINS initiated molt earlier and molted at a significantly slower rate than catbirds at BIRI. Mean individual molt durations spanned approximately 54 days at VINS and 44 days at BIRI. The two groups ended molt at about the same time. Catbirds at VINS were more variable in the timing of their molt. At both sites, second-year catbirds began and ended molt significantly earlier than after second-year catbirds. Males and females did not differ significantly in their rate or timing of molt at either site. Behavioral observations at BIRI indicated that catbirds spent less time foraging during the heaviest period of molt, but that increased foraging during late molt stages coincided with increases in fat stores, indicating overlap of molt and hyperphagy. We found no evidence that Gray Catbirds at either site departed for migration prior to completing remigial molt. The later molt schedule of BIRI birds likely resulted from the extended breeding season of some individuals. We believe that molt schedules at the two sites were influenced less by latitude per se than by site-specific differences in vegetation, food abundance, and temperature, resulting from differing elevations and conditions of coastal and inland environments.

Key words: Dumetella carolinensis, Gray Catbird, molt overlap, molt rate, prebasic molt, premigratory behavior.

INTRODUCTION

Birds molt to replace worn feathers and meet changing plumage needs. Although the benefits of molt are considerable, the costs associated with molt are high. Molt is energetically demanding, and many species increase metabolic expenditures while molting (Lustick 1970, Payne 1972, Lindström et al. 1993). Birds also have reduced flight abilities while molting flight feathers, which leads to increased risks of predation (Kjellén 1994, Slagsvold and Dale 1996). Consequently, birds must balance their need to meet the increased energetic demands of molt with the need to avoid predation.

Birds tend to segregate major events of their annual cycle, presumably because of the need to partition energetic demands (Helms 1968). Molt is a temporally variable event in most species, and it may serve as an important buffer in the

annual cycle (Noskov et al. 1999). Because rate and timing of molt can be variable within a species, individuals may adjust their molt schedule in response to specific constraints on the annual cycle. For example, a time-constrained individual could increase its rate of molt and/or overlap molt with another event in the annual cycle, such as breeding or migration. The energetic and temporal constraints of molt may also necessitate behavioral adjustments. Even though many authors have noted "skulking" behavior of birds during molt (Newton 1966, Haukioja 1971, Vega Rivera et al. 1998), few have described the behavior of actively molting birds.

No comprehensive description exists of the rate and timing of prebasic molt in Gray Catbirds (*Dumetella carolinensis*). Prior to autumn migration, adult Gray Catbirds undergo a complete prebasic molt in which all feathers, including remiges and rectrices, are replaced, whereas hatching-year birds undergo a partial molt that replaces only body feathers and selected wing coverts. Because flight feather molt imposes greater costs and higher risks than contour feather molt, adult catbirds presumably face more se-

vere constraints during their molt than do juveniles. We studied the definitive prebasic molt of Gray Catbirds, with three primary objectives: (1) to describe the overall patterns, rate, and timing of this molt, (2) to describe the behavior of adult Gray Catbirds during molt, and (3) to compare the molt regimes of catbirds from two geographically distinct breeding populations.

As latitude increases, the growing season shortens and the amount of available time to breed, molt, and prepare for migration decreases. Birds at more northern latitudes can compensate by shortening their breeding period, tolerating more overlap between phases, molting at a faster rate, and/or departing for migration later than individuals at more southern latitudes. Several studies have shown differences in molt between individuals in populations of latitudinally separated species (Mewaldt and King 1978, Mulvihill and Rimmer 1997). In addition to latitude, other factors may affect patterns of molt. We compared rate and timing of molt in catbirds at two sites that differed in latitude, elevation, proximity to the coast, and vegetation structure.

METHODS

We collected molt data on Gray Catbirds at two sites in New England. The northern site was located at the Vermont Institute of Natural Science (VINS) in Woodstock, Vermont (43°36'N, 72°32'W; elevation 320 m). Molt data were collected at VINS on a 3-ha study plot characterized by second-growth deciduous shrub-woodland, consisting of brushy thickets interspersed with groves of largely mature trees. Dominant trees included sugar maple (*Acer saccharum*), bigtooth aspen (*Populus grandidentata*), black cherry (*Prunus serotina*), and white ash (*Franxinus americana*); dominant shrubs included willow (*Salix* spp.), autumn olive (*Elaeagnus umbellata*), steeplebush (*Spiraea tomentosa*), hawthorne (*Crataegus* spp.), dwarf juniper (*Juniperus communis*), and common buckthorn (*Rhamnus cathartica*). From 1986 to 1997, 19 mist nets (12 × 2.6 m, 36-mm mesh) were operated 1 to 3 days per week during July and 5 days per week from 1 August to early November. Nets were opened for 6 hr day^{-1}, beginning 0.5 hr before sunrise, except during adverse weather conditions.

The southern site was located at the northern tip of Block Island, Rhode Island (BIRI) in Clayhead Preserve (41°12'N, 71°35'W; elevation

40 m). Block Island is approximately 2,900 ha and is located in the Atlantic Ocean approximately 19 km south of Rhode Island. The 4-ha BIRI study site was characterized primarily by early successional coastal scrubland. Dominant shrubs included northern arrowwood (*Viburnum recognitum*), black chokeberry (*Pyrus melanocarpa*), northern bayberry (*Myrica pennsylvanica*), *Amelanchier* spp., and poison ivy (*Toxicodendron radicans*). Vegetation structure differed between the two sites primarily in that BIRI lacks any dominant tree species. Data were collected at BIRI from 5 August to 30 September 1996 and 5 August to 8 October 1997. We operated 15 to 20 mist nets (12 × 2.6 m, 30-mm mesh) daily for 6–12 hr except during inclement weather.

At both sites, all captured individuals received U.S. Fish and Wildlife Service aluminum leg bands. Subcutaneous fat was assessed, and each bird was given a fat score of 0 to 6 based on the Helms and Drury (1960) scale. Birds were aged as either hatching-year or after hatching-year (adult) by skull pneumatization and eye and mouth color (Pyle 1997). At BIRI, adult catbirds received red plastic leg bands and juveniles received either white or yellow color bands; this enabled differentiation of age groups in the field. After sighting a color-banded individual, an observer used a tape recorder to note all activities of the bird while it was in view. These data were later transcribed, and we created time budgets for each bird by timing the length of each activity.

Catbirds breed at and migrate through both study sites. To determine whether catbirds overlap molt with migration, it was necessary to exclude transient birds from our analyses. We assigned cut-off dates at each site and analyzed data only from birds originally captured prior to these dates. Two criteria were used to determine site-specific cutoff dates: (1) timing of hyperphagy (the increased rate of feeding that occurs just prior to migration) and detectable fat deposition, and (2) timing of marked increases in the numbers of unbanded catbirds, presumably corresponding to an influx of migrants. Our cutoff dates are conservative, and we are confident that the birds used in our analyses were not transients. The VINS cut-off date was 15 September, whereas the BIRI cut-off dates were 23 September in 1996 and 25 September in 1997. At BIRI, we stopped color banding after these dates to

ensure that behavioral observations were record-
ed only on nontransients.

To describe the patterns of molt, we followed
the terminology of Humphrey and Parkes
(1959). We used a conventional molt scoring
system (e.g., Ashmole 1962, Newton 1966) that
assigns each remex and rectrix a score from 0
to 5 (0 = old feather not dropped, 1 = feather
missing or in pin, 2 = feather at "brush" stage
or up to one-third grown, 3 = feather one-third
to two-thirds grown, 4 = feather two-thirds to
nearly full-grown, 5 = new feather fully grown).
At BIRI, each flight feather of the right wing
and the right side of the tail were scored. At
VINS, feathers on both wings and both sides of
the tail were scored. Only the molt scores from
the right wing of each bird were used in analy-
ses. To estimate stage of molt, we calculated a
remex score by summing the scores of primaries
one to nine and the sixth secondary. We did not
include the outermost vestigial tenth primary in
the analyses because it is often difficult to ac-
curately estimate the length of this primary. This
type of remex score is often used to estimate
molt stage because it results in a more linear
relationship between molt score and date than
primary molt score alone. This linear relation-
ship is important if recapture data are used to
estimate rate of molt (Evans 1966, Newton
1966, Bancroft and Woolfenden 1982). A remex
score of 0 indicates that molt had not begun, and
a remex score of 50 indicates that molt was
complete.

When possible, catbirds were aged as either
second-year (SY) or after second-year (ASY).
Birds were aged as SY if they had been banded
in the previous year as a hatching-year bird or
if they had retained juvenal greater coverts. Ap-
proximately 88% of hatching-year Gray Cat-
birds do not molt all 10 of their greater coverts
(Pyle 1997), so an adult bird with retained ju-
venal coverts can be reliably aged as a SY. Birds
were only aged as ASY if age could be deduced
from earlier banding records (i.e., the bird was
banded in the previous year as an adult). Birds
were not aged as ASY if they had no retained
coverts, given that approximately 12% of hatch-
ing-year Gray Catbirds molt all of their greater
coverts (Pyle 1997). Birds were sexed if they
exhibited a well-developed brood patch or a clo-
acal protruberance.

STATISTICAL ANALYSES

Three methods are commonly used to estimate
rate and timing of molt: (1) regressing molt
score of individual birds on date of capture
(treating molt score as the dependent variable),
(2) regressing date of capture on molt score
(treating date as the dependent variable), and (3)
using recapture data from birds caught at least
twice during a molt cycle to determine individ-
ual rates. Each method has advantages and dis-
advantages. Regressing molt score on date pro-
vides a reliable estimate of molt duration for the
sampled population. Although this method is ap-
propriate for examining variability within pop-
ulations, it often underestimates molt rate and
therefore overestimates individual molt duration
(Pimm 1976). Treating date as the dependent
variable yields a more accurate estimate of du-
ration of molt for individuals (Pimm 1976, Ginn
and Melville 1983); however, this method does
not give a good estimate of variability within a
population. Estimates based on recapture data
also accurately estimate individual molt rates,
but such data are typically difficult to obtain.

To examine differences in duration of molt
among catbirds at VINS and BIRI, we compared
regressions of date on molt score. We then com-
pared the results of regressing molt score on date
to examine differences in population variability
between VINS and BIRI. We compared both
methods because estimates of individual and
population molt rates may differ and yield dif-
ferent insights on molt patterns in a given pop-
ulation. Although we calculated molt parameters
from recapture data for comparison, we did not
statistically compare these results due to our
small samples of recaptured birds.

For the analyses using molt score, we includ-
ed only birds in active remigial molt (remex
score from 1–49). To ensure independence of
observations, we used only one capture per in-
dividual per year on all data collected from cap-
tured individuals. If a bird was captured more
than once in a year, we randomly chose one cap-
ture to include in the analyses. To compare rate
and timing of molt between groups, we used
analyses of covariance (ANCOVA). ANCOVA
assumes that the slopes of the regression lines
are parallel (Tabachnick and Fidell 1996), there-
fore this can be used to test whether molt rates
differ between groups. If the two slopes (i.e.,
rates of molt) did not differ significantly, we

used an ANCOVA to test for differences in elevations of the regression lines to determine whether there were differences in timing of molt.

From the recapture data, birds were included only if they were examined in active molt more than once per season and at least 5 days apart. Only first and last captures were used to calculate each individual's rate of molt. We found that rate of molt slowed as birds neared molt completion, so only birds caught with a remex score < 35 were used in the analyses. We calculated molt rates by dividing the difference in remex scores by the number of days between captures. Mean dates of molt onset and completion were calculated by extrapolation from rates of recaptured birds. Duration of molt was calculated by subtracting estimated start dates from estimated end dates and determining the mean. All calendar days were calculated for non-leap years.

At BIRI, catbirds observed foraging in the field were color banded according to age, but not individually. Because we could not ascertain individual identities of foraging catbirds, we cannot guarantee that every observation was made on a different bird. Our data may thus fail to meet the assumption of independence of observations, therefore, we did not statistically compare these data. However, we believe that our large sample of observations represents accurate trends and provides valid information on catbird foraging behavior during molt. We present these results graphically and describe them in the text. The reported values are mean ± SE. We used P < 0.05 as our level of accepted significance.

RESULTS

SEQUENCE OF MOLT

The sequence of remex molt in Gray Catbirds followed the general pattern of most passerines. The innermost primary (P1) was the first to begin molting, and the primaries were replaced proximal to distal. The outermost secondary (S1) began molting at about the same time as primary 5, and secondaries 1 to 6 were replaced distal to proximal. Primary and secondary molt ended nearly synchronously. The tertials (secondaries 7 to 9) began molting at approximately the same time that primaries 2 to 4 were shed. Tertial molt typically began with the middle or innermost tertial, and the outermost tertial was the last to molt. All three tertials were fully
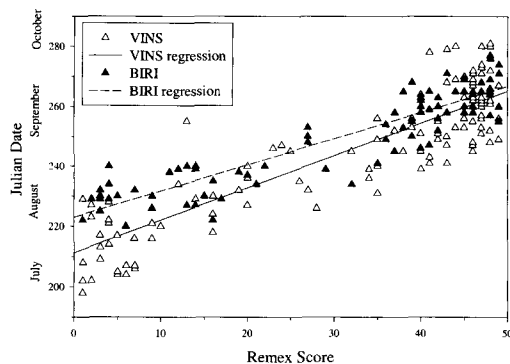

FIGURE 1. Regression of date on molt score (regression 2) for Gray Catbirds captured at VINS from 1986 to 1997, and at BIRI in 1996 and 1997. Julian date 182 = 1 July.

grown by the time primary and secondary molt was complete.

RATE AND TIMING OF MOLT

Molt rate slowed as birds reached the final stages of molt. Birds first examined with a remex score < 35 had significantly higher rates of molt than birds with initial remex scores ≥ 35 (BIRI: $t_{12} = 3.1$, $P = 0.01$; VINS: $t_{49} = 8.3$, $P < 0.001$).

Regressions of date and molt score were significant for both sites (VINS: $r^2 = 0.78$, $F_{1,127} = 456.4$, $P < 0.001$; BIRI: $r^2 = 0.83$, $F_{1,84} = 412.3$, $P < 0.001$). When date was regressed on molt score, the slope of the BIRI regression line was significantly steeper than the VINS regression line, indicating that catbirds at BIRI molted at a faster pace ($F_{1,214} = 7.6$, $P < 0.01$; Fig. 1). Based on these regressions, catbirds at VINS started molting on 31 July, whereas BIRI catbirds initiated molt on 11 August; however the two groups ended molt within two days of each other (22 September at VINS, 24 September at BIRI, Table 1). The recapture data corroborate earlier molt onset and termination dates of VINS catbirds (Table 1).

When molt score was regressed on date, the slope of the BIRI regression line was significantly steeper than the slope of the VINS regression line ($F_{1,214} = 13.0$, $P < 0.001$). This indicates less variability in the rate of molt in the population of catbirds at BIRI. This method predicted earlier onset and later termination dates than regressing date on molt score. Based on field observations, these predicted onset and termination dates were inaccurate, suggesting

TABLE 1. Rate and timing of molt of Gray Catbirds at two study sites, Vermont Institute of Natural Science (VINS) and Block Island, Rhode Island (BIRI). Population molt rate and timing were calculated by three methods: (1) regression 1 (molt score of individual birds was regressed against date), (2) regression 2 (date of capture of individual birds was regressed against molt score), and (3) recapture (mean rate and timing of molt was calculated from birds caught more than once per season during molt). Sample sizes are in parentheses.

	Molt rate (points day^{-1})	Start of molt (Julian date)	End of molt (Julian date)	Duration (days)
Regression 1				
VINS (129)	0.7	201.7	270.5	68.9
BIRI (86)	0.9	217.5	270.3	52.8
VINS SY (21)	0.8	203.7	264.4	60.8
VINS ASY (53)	0.7	204.3	274.3	70.0
BIRI SY (13)	0.7	201.7	268.9	67.2
BIRI ASY (25)	1.0	220.6	273.1	52.5
VINS female (53)	0.8	207.4	271.2	63.8
VINS male (29)	0.7	196.3	271.7	75.4
BIRI female (20)	0.8	216.4	278.1	61.7
BIRI male (14)	1.0	220.8	270.1	49.3
Regression 2				
VINS (129)	0.9	211.3	265.3	54.0
BIRI (86)	1.2	222.9	266.8	43.9
VINS SY (21)	1.0	210.2	259.0	48.8
VINS ASY (53)	0.9	215.1	296.6	54.5
BIRI SY (13)	0.9	210.1	266.1	56.0
BIRI ASY (25)	1.1	225.3	270.1	44.8
VINS female (53)	1.0	214.5	264.5	50.0
VINS male (29)	0.9	207.3	266.3	59.0
BIRI female (20)	1.1	222.5	268.5	46.0
BIRI male (14)	1.2	223.5	266.6	43.1
Recapture				
VINS (39)	0.9 ± 0.0	208.6 ± 1.9	264.0 ± 1.6	55.3 ± 1.2
BIRI (11)	0.9 ± 0.1	211.4 ± 4.0	271.4 ± 2.2	60.0 ± 4.4
VINS SY (9)	0.9 ± 0.0	207.7 ± 3.7	262.5 ± 3.8	54.9 ± 2.0
VINS ASY (15)	0.9 ± 0.1	215.0 ± 2.9	270.2 ± 2.2	55.2 ± 2.5
BIRI SY (3)	0.8 ± 0.1	202.4 ± 9.5	270.2 ± 3.5	67.8 ± 9.4
BIRI ASY (2)	0.9 ± 0.1	220.7 ± 1.2	276.9 ± 2.9	56.2 ± 4.1
VINS female (20)	0.9 ± 0.0	211.2 ± 2.6	265.6 ± 2.6	54.5 ± 1.1
VINS male (9)	1.0 ± 0.1	208.1 ± 4.5	262.0 ± 2.4	54.0 ± 3.9
BIRI female (6)	0.9 ± 0.1	213.0 ± 4.4	271.2 ± 3.9	58.3 ± 6.7
BIRI male (3)	0.8 ± 0.1	208.8 ± 12.1	272.4 ± 3.0	63.6 ± 9.3

that regressing molt score on date underestimated mean population molt rates in our samples.

AGE AND SEX DIFFERENCES IN RATE AND TIMING OF MOLT

Regressions of date and molt score were significant for both age groups at both sites ($r^2 \geq 0.78$, all $P < 0.001$). When date was regressed on molt score, the slopes of the regression lines were not significantly different between age groups for either site (VINS: $F_{1,73} = 0.7$, $P = 0.40$; BIRI: $F_{1,37} = 1.7$, $P = 0.21$), but the elevations of the regression lines did differ significantly (VINS: $F_{1,73} = 10.8$, $P < 0.01$; BIRI: $F_{1,37} = 9.7$, $P < 0.01$; Fig. 2). This indicates that

individuals in both age groups molted at about the same rate, but that SY catbirds began and ended molt earlier than ASY catbirds (Table 1). Recapture data yielded similar results, with the mean onset and termination dates of molt always earlier for SY catbirds than for ASY individuals (Table 1). At both sites, regressions of molt score on date revealed slopes that did not differ significantly between age groups (VINS: $F_{1,73} = 1.3$, $P = 0.26$; BIRI: $F_{1,37} = 2.1$, $P = 0.17$), indicating that neither SY nor ASY catbirds were more variable in molt synchrony.

Regressions of date on molt score were significant for both sexes at both sites ($r^2 \geq 0.78$, all $P < 0.001$). At both sites, regressions of date
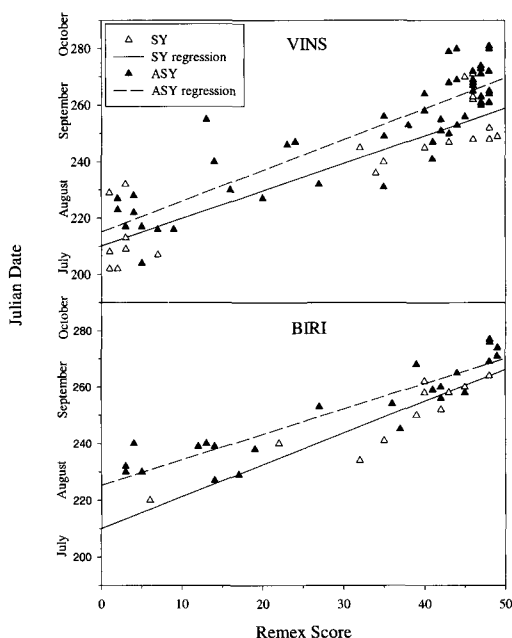
FIGURE 2. Regression of date on molt score (regression 2) for second-year (SY) and after second-year (ASY) Gray Catbirds captured at VINS from 1986 to 1997, and BIRI in 1996 and 1997.

FIGURE 3. Percent of Gray Catbirds caught as a function of remex score at VINS from 1986 to 1997 and at BIRI in 1996 and 1997.

on molt score yielded no significant differences in slopes or elevations of regression lines between sexes (all $P \geq 0.2$, Table 1). This indicates that males and females did not differ in their rates or timing of molt. Regressions of molt score on date also showed no differences in slope or elevations of regression lines (all $P \geq 0.1$), indicating that neither population was more variable in its timing of molt. Recapture data similarly indicated no differences in molt rate and timing between the sexes (Table 1).

BEHAVIOR OF GRAY CATBIRDS DURING MOLT

At both sites, many more Gray Catbirds were captured in early (remex scores ≤ 20) and late (remex scores > 35) stages of prebasic molt than during mid-molt (Fig. 3). The fewest number of birds were caught with remex scores of 21 to 35, corresponding to their period of heaviest molt when flight maneuverability is most severely impaired. In addition to restricting their movements, catbirds at BIRI spent less time foraging during the heaviest stages of molt, then increased their foraging during late molt stages (Fig. 4a). This increase coincided with signifi-
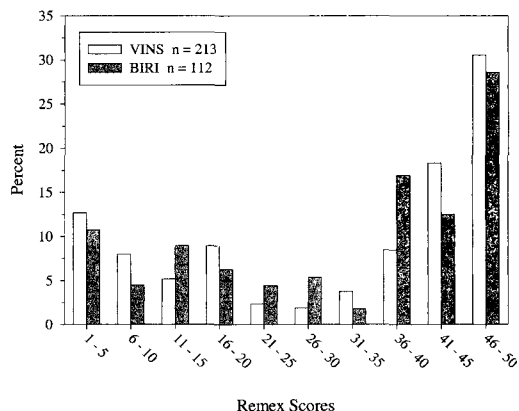
cant increases in fat stores, suggesting that adult catbirds begin pre-migratory fat deposition during their final stages of molt (Kruskal–Wallis test, $H_8 = 42.6$, $P < 0.001$; Fig. 4b). At both sites, catbirds steadily increased their body mass as molt progressed (Fig. 5). In 9 of the 11 groupings of remex scores that we compared, catbirds at BIRI had higher body masses than catbirds at VINS (Fig. 5).

OVERLAP OF MOLT WITH MIGRATION

We found no evidence that Gray Catbirds at either site departed for migration prior to completing remigial molt. Twenty-eight adult catbirds at VINS and 10 adult catbirds at BIRI were captured prior to southward departure with completely new flight feathers (remex score = 50).

DISCUSSION

RATE AND TIMING OF MOLT IN THE ANNUAL CYCLE

Gray Catbirds in New England undergo their prebasic molt after breeding and prior to departing for autumn migration, a pattern similar to that of most Nearctic-Neotropical migratory passerines. Catbirds had a significantly slower rate of molt after attaining a remex score of 35, indicating that they had fewer remiges growing and, consequently, fewer and smaller wing gaps. Birds with fewer wing gaps are less constrained by the reduced flight efficiency imposed by heavy molt (Hedenström and Sunada 1998). After reaching remex scores of 35, catbirds spent more time foraging and began to deposit fat
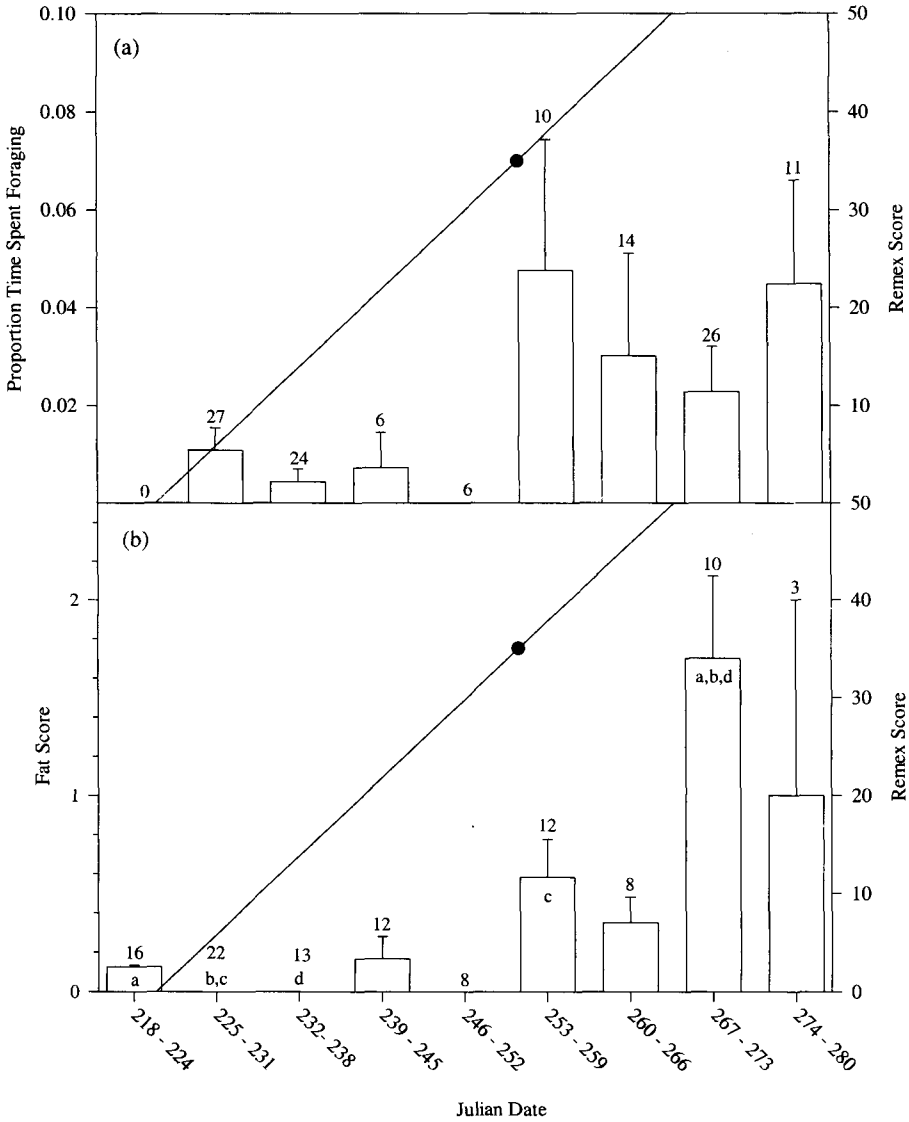
FIGURE 4. Mean ± SE (a) proportion of time spent foraging, and (b) fat score of adult Gray Catbirds at BIRI during week-long periods in 1996 and 1997. In panel (b), bars with the same letters are significantly different when Mann–Whitney U-tests with sequential Bonferroni correction are used for post-hoc testing. The line for the mean remex score is the regression line calculated when date is regressed on molt score (regression 2). The solid circle indicates a remex score of 35. Numbers above bars are the number of birds observed.

stores, indicating overlap of final molt stages with hyperphagia.

Although individuals of some species, especially those breeding at high latitudes, regularly begin migrating during the final stages of prebasic molt (Dolnik and Blyumenthal 1967, Rimmer 1988), catbirds at VINS and BIRI did not appear to initiate migration before completing molt. Locally-breeding adults at both sites were captured in freshly-molted basic plumage after the extrapolated mean end dates of molt (22 September at VINS, 24 September at BIRI). Moreover, of approximately 800 Gray Catbirds examined in 1994 and 1995 at a migratory stopover site at Fort Morgan, Alabama (30°13′N, 88°00′W), only 2 showed active remigial molt; in both cases molt was nearly complete and limited to the proximal few secondaries (D. Cim-
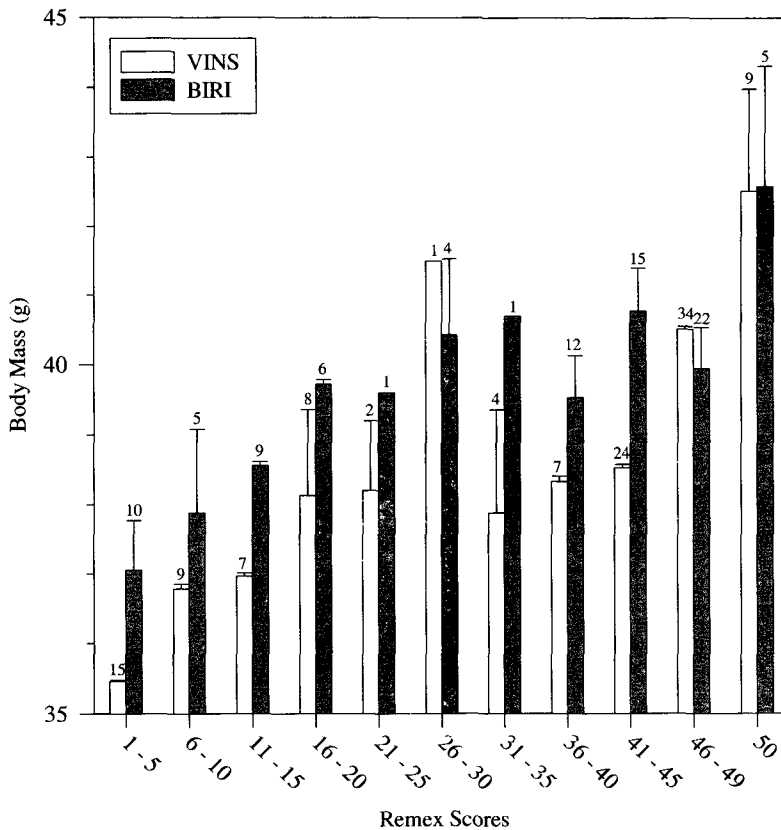
FIGURE 5.   Mean ± SE body mass of adult Gray Catbirds caught during different stages of molt at VINS from 1986 to 1997, and at BIRI in 1996 and 1997. Numbers above bars are sample sizes.

prich, pers. comm.). It thus appears that Gray Catbirds rarely overlap molt and migration.

It is more common for passerines to overlap molt with breeding than with migration (King 1974). Several species, including Lesser Redpolls (*Carduelis flammea cabaret,* Evans 1966), Yellow Warblers (Rimmer 1988), White-crowned Sparrows (*Zonotrichia leucophrys,* Morton and Morton 1990), and Northern Mockingbirds (*Mimus polyglottos,* Zaias and Breitwisch 1990), begin molting while feeding fledglings. Late-breeding individuals often exhibit greater overlap between breeding and molt (Hemborg 1998). We did not collect breeding information at either site, but we obtained evidence that some catbirds at BIRI bred late in the season. A female with a receding brood patch and no signs of active molt was captured at BIRI on 11 September 1996 with two juveniles judged to be only 1 to 3 days out of the nest. Another female catbird was captured on 10 Au-

gust 1997 at BIRI with an egg in her oviduct and was presumably still laying. The earliest that young could have fledged from her presumed nest was 28 August. Second broods of Gray Catbirds are known to fledge between mid-July to early August in Michigan and Manitoba, and third broods fledge during early September in South Carolina and Arkansas (Cimprich and Moore 1995). Our documentation of a female with dependent fledglings on 11 September in Rhode Island seems exceptionally late, and we expect that this female began molt shortly after we captured her, while still feeding fledged young. Such late-breeding individuals might be forced to overlap breeding with molt because of time constraints.

BEHAVIOR DURING MOLT

Molt is energetically costly. Molting individuals can meet higher energetic demands by increasing energy input (obtaining more food) or de-

creasing energy loss (conserving energy). However, molting birds must also cope with impaired flight abilities, which presumably affects foraging efficiency and predator avoidance. Gray Catbirds at BIRI were detected and caught less often during the period of heaviest molt, a result consistent with the skulking behavior reported in heavily-molting individuals of other species (Newton 1966, Haukioja 1971, Vega Rivera et al. 1998). The catbirds that we observed spent less time foraging in mid stages of molt than in later stages, when they became hyperphagic. Although it is possible that catbirds foraged in more protected sites during mid-molt and escaped our detection, we believe that this was unlikely. We spent extended periods searching for catbirds each day and observed no evidence of any switches in foraging locations. Instead we believe that skulking behavior may be a response to minimize predation risks or a means to reduce energy expenditure in the face of increased energetic demands of molt. Catbirds did not lose mass while molting, suggesting that skulking behavior may effectively conserve energy during heavy molt. This is difficult to test and we encourage investigations of behavior patterns during molt in other species.

AGE AND SEX DIFFERENCES IN MOLT

At both sites, SY catbirds began and ended molt earlier than ASY individuals. Yearling males begin molting earlier than older birds in some species, presumably because young males are less likely to obtain mates and therefore are not often constrained by the need to care for young (Rimmer 1988, Morton and Morton 1990, Hemborg et al. 1998). In addition, breeding success is often age dependent (Perrins and Birkhead 1983, Harvey et al. 1985). If SY catbirds experience lower nesting success than ASY catbirds, an earlier termination of breeding activities might enable failed breeders to begin molting earlier. SY birds may be less likely than ASY breeders to attempt a second or third brood. A bird that molts early may be able to spend more time depositing fat, enabling it to depart on migration earlier and/or in better condition. There is evidence that Gray Catbirds defend winter territories (Rappole and Warner 1980), so early migration and subsequent early arrival on the wintering grounds might be advantageous for an individual seeking to secure a high quality territory.

Rate and timing of molt often vary between males and females (Rimmer 1988, Morton and Morton 1990, Hemborg 1998), but in some species these parameters are similar between sexes (Zaias and Breitwisch 1990, Thompson 1991). Sex-related differences in timing of molt are usually attributed to one sex having a greater or more extended role in parental care. Timing and rate of molt did not differ between male and female Gray Catbirds in our samples. Both sexes feed nestlings (Cimprich and Moore 1995), but it is unknown whether males and females play equally active roles in fledgling care. Our results suggest that neither sex experiences an earlier release from the constraints of parental care.

DIFFERENCES BETWEEN SITES

As a consequence of a later breeding season, birds at more northern latitudes may begin molting later (Mewaldt and King 1978, Underhill et al. 1992, Mulvihill and Rimmer 1997), molt at a faster rate (Evans et al. 1967, Mewaldt and King 1978), and be more likely to overlap molt with breeding or migration (Dolnik and Blyumenthal 1967). Gray Catbirds at the more northern VINS site molted at a slower rate than catbirds at BIRI, and no individuals in either population appeared to overlap molt with migration. Our results depart from those of other studies that have compared timing of molt between latitudinally separated sites. Instead of starting molt later, the more northern Vermont population molted slightly earlier than the Rhode Island population. Higher latitude populations of Red-eyed Vireos (*Vireo olivaceus*) have been shown to molt later than populations 3.3° of latitude to the south (Mulvihill and Rimmer 1997), but other studies describing latitudinal differences in timing of molt have compared populations separated by at least 10° of latitude (Mewaldt and King 1978, Underhill et al. 1992). VINS and BIRI are separated by only 2.3° of latitude, and this difference alone may have been too small to account for variations in molt rate and timing between the two populations of catbirds we studied.

Other differences between the two sites probably contribute to the later molt schedule of catbirds at BIRI. BIRI is a coastal site, whereas VINS is inland. Coastal sites tend to have later spring phenologies than inland sites at comparable latitudes, because cold ocean water retards the advance of spring. Spring phenologies at

VINS and BIRI may be similar, and catbirds at each site may start breeding at approximately the same time. However, differences in vegetation and proximity to the coast may afford catbirds at BIRI the opportunity to breed later into the fall than catbirds at VINS. Gray Catbirds are primarily frugivorous during autumn (Cimprich and Moore 1995). Fruit is abundant at the coastal scrub BIRI site until at least the beginning of October (Parrish 1997), by which time most catbirds have departed for migration. Whereas fruit appears plentiful at VINS during autumn (C. Rimmer, pers. observ.), catbirds at BIRI may be able to obtain relatively more food, as evidenced by their consistently higher body masses throughout the season. Fruit also may be plentiful later in the fall at BIRI than at VINS. VINS is an inland site at higher latitude and elevation than BIRI, and frosts are earlier and heavier at VINS. It is likely that fruit production and availability declines after frosts. On cold mornings, birds may have to spend more energy thermoregulating and may receive a lower net energy gain from food intake. Thus, it may be more advantageous for catbirds at VINS to end breeding earlier than birds at BIRI.

Gray Catbirds at BIRI may capitalize on that site's later autumn phenology and breed later into the season than birds are able to at VINS. We obtained incidental evidence of late season breeding by some Gray Catbirds at BIRI, yet no similar evidence at VINS, despite regular operation of the VINS banding station throughout every summer and fall season from 1986 to 1997. The later start of molt by BIRI birds likely results from the extended breeding season of some individuals and/or later migration departures. The latitudinal difference of less than 3° between VINS and BIRI probably exerted little influence on the relative timing and rate of molt in Gray Catbirds at the two sites. Instead, we believe that molt schedules were influenced by site-specific differences in vegetation, food abundance, and temperature, due primarily to differing conditions of coastal and inland environments.

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