

THE AUK

A QUARTERLY JOURNAL OF
ORNITHOLOGY

VOL. 88

JULY 1971

No. 3

MOLT AND THE ANNUAL CYCLE OF THE CHUCK-WILL'S-WIDOW, *CAPRIMULGUS CAROLINENSIS*

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THE family Caprimulgidae consists of about 73 species of nocturnal and crepuscular birds commonly called nightjars from their persistent penetrating nocturnal calls. They are divided into two subfamilies, the Chordeilinae, a group of 8 New World species, and the Caprimulginae, a group of approximately 65 species occurring in most of the warmer land areas of the world. The chordeilines are largely crepuscular in their habits, some species being active on overcast or, occasionally, sunny days; most of the caprimulgines are much more nocturnal than the chordeilines. The Chuck-will's-widow (*Caprimulgus carolinensis*) is the largest member of its genus, which contains some 40 African, Eurasian, and New World species (Peters, 1940). It is a common breeding bird of the deciduous forests of the southern third of eastern North America, and winters largely in the Antilles, Central America, and the southernmost areas of eastern North America.

The sequence of molt has been described for several African and Eurasian caprimulgines (Verheyen, 1956; Stresemann and Stresemann, 1966) and partially described for the chordeiline Common Nighthawk (*Chordeiles minor*) by Selander (1954). Some intriguing variations exist in the sequence and timing of molts among the caprimulgiforms (Stresemann and Stresemann, 1966; Rohwer, MS on *Phalaenoptilus nuttallii*), and knowledge of the sequence and time of feather replacement for more caprimulgiforms, coupled with information on their breeding schedules, food resources, and distribution, will undoubtedly lead to a better understanding of the biological significance of these variations.

Surprisingly, the factors influencing the scheduling of the molt relative to reproduction and, in migratory species, to the fall departure are seldom investigated. Molt is an energy-demanding aspect of the summer life of many birds, and Pitelka (1958) suggests that its scheduling may correspond more closely to the time of maximal food abundance than does

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the period when young are being fed in Steller's Jays (*Cyanocitta stelleri*) of the Queen Charlotte Islands. At present our knowledge of the timing of the molt in caprimulgids is limited to the information that some molt on their breeding grounds and others on their wintering grounds.

As part of a general examination of morphological variation in the Chuck-will's-widow, I have examined most of the skins of this species in North American museums. The first part of this paper describes its molts in detail and substantiates the existence of a distinctive first winter, or Basic I, plumage (Humphrey and Parkes, 1959; Palmer, 1962: 2-3). The second part treats in detail the timing of events during the breeding season: arrival, egg laying, molt, and departure south. In this section I also attempt to explain why the molt occurs on the breeding grounds at the apparent expense of raising an additional brood, and to explain some interesting differences in the distribution of adults and subadults over the wintering grounds. Data were obtained entirely from preserved skins, public and personal files, and egg collections. Because they are based on large samples the schedules of events on the breeding grounds should be more accurate than could be obtained from the field study of a local population. The nocturnal habits and large territories of the Chuck-will's-widow would make it extremely difficult, even with full-time field work, to obtain such information on more than a few pairs per season.

METHODS AND TERMS

In all, 560 specimens were examined: 110 of these, collected from 1 October to 15 March, came largely from the wintering grounds; the remaining 450, collected from 16 March to 30 September, came largely from the breeding range. Almost all 560 specimens were checked for molt, and all specimens undergoing primary molt were examined as thoroughly as possible for feather replacement. Feather wear and fading appears to be minimal in the Chuck-will's-widow (hereafter often referred to as "Chuck"), and frequently it was difficult to distinguish new from old feathers, especially among the remiges. For this reason I nearly always checked the insertions of the remiges to detect the presence of any flakes of sheathing that might still be attached to the base of recently replaced feathers. Empty sockets and feathers showing only as buds were also easily detected in this manner.

To examine insertions of the primaries, I unfold the wing a slight distance from the body and insert an index finger to hold the humerus or end of the ulna firmly against a table. This pressure eliminates the possibility of tearing the skin as the wing is bent slightly farther downward with the other three fingers or thumb. With the wing in this position

the under primary coverts can be folded back with a straight forceps to reveal the insertions of all 10 primaries.

The insertions of the secondaries were examined by bending all the upper secondary coverts back with a straight forceps. Again the wing must be held securely while lifting the coverts to avoid damaging the specimen. Lifting the secondary coverts in this manner kinks them near their insertions, but when done with care does not seem to harm them as they are easily rearranged properly.

Throughout this paper birds that have completed the post-juvinal molt but that are less than a year old (or at most just over a year old) are referred to as subadults. The timing of the molt of the secondaries, rectrices, and contour feathers is given in relation to the outermost incoming primary. Hereafter any primary I refer to may be assumed to be the outermost incoming primary unless otherwise noted. Primaries, secondaries, and rectrices are referred to by the capital letters P, S, or R with numerals indicating specific feathers; unless otherwise indicated these notations refer to both left and right feathers. Where particular specimens are referred to, the names of the institutions where they are housed are listed in the "Acknowledgments."

MOLTS AND PLUMAGES

Nowhere has the sequence of plumages been treated fully for the Chuck-will's-widow. Bent (1940) wrote briefly on its sequence of plumages, but without supplementary information his account is confusing. My additional information on the sequence of plumages in the Chuck clarifies Bent's account, and I believe he had a fairly clear understanding of its plumage sequence. His failure to state what is now obvious—that males have dark rectrices until they are about a year old—has probably caused his poorly worded account to be disregarded. Forbush (1927: 299) correctly stated that the sexes are alike in the first winter and juvinal plumages, but erred in saying they are similar to the adult female in pattern and color (the juvinal plumage is very different from that of first winter or adult birds; Ridgway, 1914). Despite this error, Forbush's statement clearly indicates that males lack white in their lateral rectrices for their first year. Not only Bent, but also all other subsequent authors have overlooked this point.

The natal down.—The natal down of the Chuck-will's-widow is a golden brown, darker above than below, and usually darkest on the lower back (see Bent, 1940). I have compared four downy chicks sexed as males with two sexed as females and found no dimorphism in their coloration.

Replacement of the natal down.—I examined only one specimen taken at the beginning of the replacement of the natal down by the juvinal

plumage (UOMZ 2172, ♂, wt. 40.9 g); it was probably between 6 and 10 days old when collected. Its juvenal primaries and secondaries are just emerging from their sheaths and its rectrices are entirely ensheathed and hidden by down. The greater and lesser upper wing coverts, the feathers of the humeral tract, and those of the ventral tract from its bifurcation on the neck to midway down the belly are emerging from their sheaths, many having tufts of down attached to their tips. The juvenal feathers of the femoral and dorsal tracts are entirely sheathed, but the sheaths are relatively large. The tail coverts and the feathers of the posterior ventral tracts, throat, top of the head, auricular, and ocular regions are showing only as very small sheaths. Not even the buds of feathers are yet showing for the rictal bristles or in the crural regions and on the tarsi.

The juvenal plumage.—The Chuck's juvenal body plumage is a light ochreous buff in general color, strikingly different from either the first winter or adult plumages. I compared six specimens largely in juvenal plumage—three of each sex—and found no sexual dimorphism in this plumage. Thus, Ridgway's (1914) description of the plumage of the "young female" appears to stand equally well for either males or females in juvenal feather.

Replacement of the juvenal plumage.—I have seen 14 specimens either entirely or partially in juvenal plumage. Replacement of the juvenal body feathers probably begins before the young birds can fly, as indicated by a specimen (UOMZ 3019) with a 131-mm wing ($\frac{2}{3}$ grown) and a 50-mm tail ($\frac{1}{3}$ grown) that was beginning to replace its juvenal plumage. (In this specimen the emerging rictal bristles are about $\frac{1}{4}$ their full length and sheathed at their bases.) Replacement of the juvenal plumage begins about simultaneously in the middle upper secondary coverts, the middorsal tract, and malar region. It is next apparent in the ventral tract immediately posterior to its bifurcation. Replacement then progresses posteriorly down the dorsal tract and simultaneously proceeds forward over the crown. The juvenal feathers of the throat and the tertials and greater secondary wing coverts appear to be the next feathers replaced, although at this point my series had a slight gap in the ages of the birds. Last to be replaced are the juvenal feathers of the crural, femoral, and lower ventral tracts and the upper and under tail coverts. The replacement of the buffy juvenal body feathers during the postjuvenal molt must always be complete, as I have never seen a fall specimen showing any trace of these feathers in its plumage.

In young that have not started the postjuvenal molt the primary coverts, alulae, tarsal feathers, and several rows of lesser secondary coverts are similar in coloration to the first winter plumage. None of the speci-

mens replacing the distinctively light colored feathers of their juvenal plumage showed evidence of replacing any of these dark feathers or their rectal bristles. This and the dark coloration of these feathers strongly suggest that they are retained as part of the first winter plumage, as are the juvenal primaries, secondaries, and rectrices.

Sutton (1941) described the molts and plumages of the young Whip-poor-will (*Caprimulgus vociferus*); I can find no difference in the extent of the postjuvenal molt of this species and the Chuck-will's-widow. The only point missing in the comparison is the fate of the juvenal tarsal feathers in the Whip-poor-will. Young Chucks that have begun molting into the first winter plumage wear parts of three plumages: natal down on the tarsi and ventral apterium, juvenal feathers not yet replaced or not to be replaced in the postjuvenal molt, and first winter feathers that have already replaced juvenal feathers. Sutton (1941) describes a similar overlap in the plumages of young Whip-poor-wills.

The first winter plumage.—Subadult Chucks of both sexes resemble normal, dark-tailed adult females in general color pattern. Very rarely, subadult males and adult females show a small diffuse patch of white within the inner webs of one, or sometimes two or three, of their outermost rectrices. First-year male Chucks ordinarily have no white in their outer rectrices, and the sexes show no apparent plumage dimorphism in first winter plumage.

Subadults of both sexes can usually be distinguished from adult females by the following four plumage characters given in order of importance. (1) The rectrices of both males and females that are at least partially clothed in the light ochreous buff juvenal plumage are noticeably narrower and more pointed than they are in females known to be adults because of the presence of worn body feathers (see 3 below). As the rectrices are not replaced in the postjuvenal molt and as no winter molt occurs, age classes can be distinguished by this character for approximately a year. Dickey and van Rossem (1938) have also noted that young Pauraques (*Nyctidromus albicollis*) in first winter plumage "may be distinguished from adults by the narrower, more pointed, and usually impurely colored tail feathers." With experience one can probably age most Chucks by the width and pointedness of their rectrices (Figure 1). (2) The innermost three secondaries of first-year birds are usually contrastingly lighter than their other secondaries, tertials, and back feathers. These secondaries are typically intermediate in coloration between the buffy juvenal body feathers and the normal color of adult secondaries. (3) As noted above, the replacement of the ochreous buff body feathers of the juvenal plumage (Ridgway, 1914) appears always to be complete. Many specimens will show a few to many body feathers that are con-

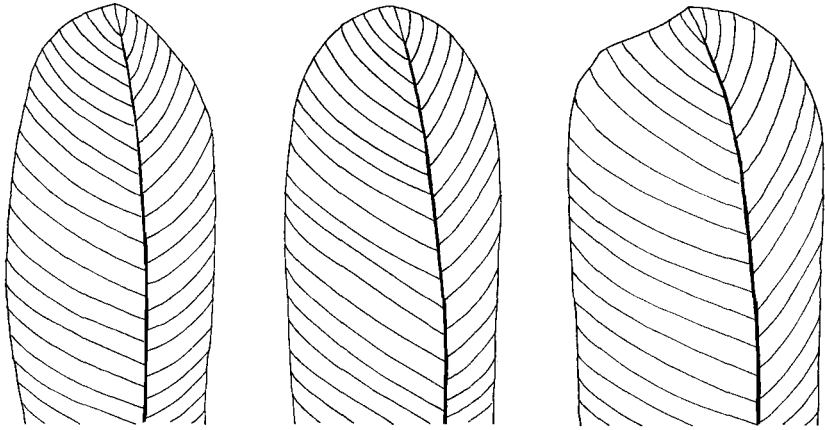


Figure 1. Dorsal views of the outermost left rectrix of three male Chuck-will's-widows. The right-most feather was drawn from a typical adult (USF-SAR 50), and the left-most from a typical subadult (CU 3631). The center figure was drawn from a bird (LSU 33855) that would be somewhat difficult to distinguish from adult females on the basis of rectrix size and shape alone.

trastingly more worn than adjacent feathers of the same type. As these are always dark feathers, typical of the adult or first winter plumage, these birds must be over a year old. Thus birds showing worn body feathers are adults, but the converse is not necessarily true, as some males with white in their outer three rectrices will show no worn body feathers. These worn feathers are usually immediately apparent in the posterior ventral tracts but, if not evident here, they should also be sought among the rump feathers. (4) The general coloration of subadults is typically darker than adults. This character is quite variable and of little use in the determination of age.

Because of the importance of the width of the lateral rectrices in aging Chucks, I quantified this character by measuring the length of the barbs in the inner vane of one of the fifth rectrices 4 to 5 cm from the tip of the feather. A sharp pencil is inserted in the barbs adjacent to the rachis and a line drawn parallel to the barbs, dividing them to their tips. The length of this line was then measured to the nearest half-millimeter. Of 52 specimens sexed as males and having no or virtually no white in their lateral rectrices, the mean barb length was 32.8 mm (SD = 2.68); of 206 specimens sexed as males and having prominent white areas in their lateral rectrices, the mean barb length was 39.1 mm (SD = 2.65).

As noted above the few available specimens sexed as females and being at least partially clothed in their light juvenal body feathers had narrow,

pointed rectrices similar to those of dark-tailed, subadult males. It seemed desirable therefore to present statistics on the barb length of samples of presumed subadult and adult females. These samples were assembled on the basis of the 2nd and 3rd age characters given above. The samples are much smaller than those for the males for two reasons; first, distinguishing characters (2) and (3) were not discovered until about half the specimens had been measured, and second, specimens were included only if both of these characters indicated the same age determination. Thus the sample of presumed adult females was composed only of birds with dark innermost secondaries and some worn body feathers, and the sample of presumed subadult females was composed only of birds with light innermost secondaries and no worn body feathers. It should be emphasized that not all birds can be aged by the color of their innermost secondaries, and that some birds with no worn body feathers must be adults; thus it is impossible to be certain of the purity of the sample of subadult females. On the basis of these characters samples of 26 presumed subadult and 36 adult females were assembled. The mean for the subadults was 31.7 mm (SD = 2.73) and for adults was 37.0 mm (SD = 2.80).

The difference between the barb lengths of presumed older females and younger females is highly significant ($P < 0.001$) as is that between presumed older females and subadult males ($P < 0.001$). Despite these highly significant differences, it is sometimes difficult to be certain of the age of a single bird on the basis of barb length alone because the distributions of barb measurements for both sexes of subadults overlap fairly broadly with the distribution for adult females. An F_{\max} -test showed no significant differences in the variances of the four sex and age classes. Therefore the best prediction of the age and sex of a dark-tailed bird is the class whose mean barb length that of the bird in question most closely approximates.

Molts and plumages of adults.—This section treats the annual molt, including the Prebasic II or second autumn molt, by which subadults attain their first fully adult plumage. As Ridgway's (1914) description of adult plumages appears to be quite satisfactory the following sub-headings deal only with molt. Robbins et al. (1966: 168) state that the Chuck-will's-widow is sexually dimorphic in the coloration of the narrow throat band. While females do tend to have slightly buffier throats than males, the sexes overlap so broadly in this character that is virtually useless for sexing individuals.

Adult Chucks have but one molt a year, in middle and late summer. Of the many winter specimens examined for molt, only one, a male lacking white in its lateral rectrices (AMNH 477288, Marco, Florida, February 1886), showed nonadventitious feather replacement. On this specimen

P1 and P2 were new and P3, P4 and P5 were incoming. With the exception of the new primaries, its plumage was unusually worn. This and the absence of white in its lateral rectrices suggest that it was about a year and a half old, and that the timing of its molt was late rather than early.

Subadults entering their second autumn molt can be separated from adults at least until P7 is being replaced as the subadult characters are not lost before this stage of the molt. I have found no difference in the sequence of feather replacement for the two age classes in the portion of the molt that occurs before the replacement of P7. Therefore subadults have not been distinguished from adults in most of the following discussion.

Unfortunately my sample of molting specimens was too small to allow a direct estimate of the duration of the molt. An indirect estimate of 3 to 4 months is made in the second part of this paper.

MOLT OF PRIMARIES. Chucks replace their primaries in a simple descending sequence starting with the innermost primary, P1, and ending with P10. This is similar to the sequence in other caprimulgids studied by the Stresemanns (1966) that lack primaries highly specialized for display. Surprisingly, Chucks frequently have two, three, or even four adjacent primaries growing at the same time, sometimes resulting in large gaps in the wing surface. Almost invariably the innermost of a series of incoming primaries is longer than the outermost, indicating that adjacent feathers are seldom dropped simultaneously, even though they often appear to have been lost in quick succession. Unfortunately my sample of birds replacing primaries was much too small to check for any north-south variation in the rate of primary replacement.

Table 1 summarizes part of my data on simultaneous replacement of adjacent primaries. It presents the percentage of specimens showing more than a single growing primary for the various stages of the primary molt. Thus specimens that were replacing only P1 and specimens whose molt was nearly completed (P10 nearly full length) were not included in calculating the percentages, because they do not show more than a single growing primary. In the few specimens where the replacement of primaries was not symmetrical, the most advanced wing was scored. The first column (N) of this table stands for the outermost primary being replaced. Any bird whose outermost missing or incoming primary was number 4, for example, would be entered only in the fourth primary row (number 4 under N); if only P4 were less than full length the bird would be tallied in the P_N column, but if P4 and P3 were less than full length it would be tallied in the P_{N-1} column, etc. For each primary row the percentages of individuals growing one, two, or more primaries has been calculated.

TABLE 1
THE TENDENCIES OF CHUCK-WILL'S-WIDOWS TO HAVE MORE THAN ONE GROWING
PRIMARY¹

| Outermost growing primary (N) | P _N | P _{N-1} | P _{N-2} | P _{N-3} | P _{N-4} | Total specimens |
|--|--------------------|------------------|------------------|------------------|------------------|--------------------|
| P1 | 100 (7+6) | | | | | 13 |
| P2 | 0 | 100 (16+1) | | | | 17 |
| P3 | 0 | 15 (2+0) | 85 (10+1) | | | 13 |
| P4 | 13 (1+1) | 20 (3+0) | 47 (6+1) | 20 (3+0) | | 15 |
| P5 | 0 | 38 (3+0) | 38 (3+0) | 12 (1+0) | 12 (1+0) | 8 |
| P6 | 14 (1+0) | 29 (0+2) | 43 (3+0) | 14 (1+0) | 0 | 7 |
| P7 | 11 (1+0) | 67 (3+3) | 11 (1+0) | 11 (1+0) | 0 | 9 |
| P8 | 0 | 0 | 0 | 0 | 0 | 0 |
| P9 | 0 | 100 (1) | 0 | 0 | 0 | 1 |
| P10 | 33 (3) | 67 (6) | 0 | 0 | 0 | 9 |
| | | | | | | — |
| | | | | | | 92 |
| Totals | 5 (4) ² | 53 (40) | 33 (25) | 8 (6) | 1 (1) | 76 ² |

¹ The large numbers are percentages while the numbers in parentheses are category totals. Separate totals for subadults and adults, respectively, are given through P7. All percentages were calculated from row totals. See text for further explanation.

² These totals are exclusive of the 13 specimens in row 1 and the 3 specimens in the P_N column of row 10. The latter three all had P10 virtually fully grown and could not have been growing P9 also.

The number of specimens in each category is given in parentheses beside the percentages. Adults and subadults are separated through P7, the first number being for adults and the second for subadults.

Scanning of the columns in Table 1 indicates that Chucks show no tendency to grow fewer primaries simultaneously as the molt proceeds outward as far as P7. Unfortunately almost no Chuck specimens were replacing P8 and P9 (see "Summary of molt in adults") which makes it impossible to determine whether or not this trend continues when the longest feathers of the wing are being replaced. On the sole specimen available that was replacing P9 (GMS 12195), this primary was entirely sheathed in both wings, and P8 was about 4 cm less than full length, indicating that this bird dropped P9 when P8 was less than half grown. The available specimens with only P10 incoming usually had this feather nearly full length and do not, therefore, provide evidence against the continued presence of two to three growing primaries when P8, P9, and P10 are being replaced.

Excluding specimens molting only P1 and specimens on which P10 was nearly full length, I calculated the percentages of birds growing 1, 2, 3, 4, or 5 feathers at a time. These percentages and the totals used to

calculate them are given in the bottom row of Table 1. More birds show two incoming feathers than three, but there are more possible combinations of two primaries than of three. In any case, these percentages show clearly that Chucks more often have two or three growing primaries than one. With these percentages at hand it is interesting to note the average number of primaries missing per wing in Chucks whose molt had advanced beyond P1 but was not yet almost completed. For many of the specimens used in calculating the percentages in the bottom row of Table 1, I was able to measure the missing proportion of each molting primary. The sum of these proportions for a specimen gives a good indication of how much primary surface is missing in each wing. On the average Chucks were missing the equivalent of 1.67 primaries per wing; as the magnitude of this average indicates, specimens missing the equivalent of over 2 primaries per wing were common.

MOLT OF SECONDARIES. The normal number of secondaries appears to be 12 in Chucks, although occasional specimens had 13. The Stresemanns (1966: 378) record that the Pennant-winged Nightjar (*Cosmetornis vexillarius*) typically has 12 secondaries, but they note parenthetically that one specimen had 13. Possibly Chucks always have 13, the innermost usually being so small that it is mistaken for a covert or tertial. In any event, this has little bearing on the molt.

Replacement of the secondaries begins when P6 or P7 are coming in. Of nine specimens just beginning secondary replacement, seven were growing P6 and two were growing P7. Eight specimens replacing P5 were examined for secondary molt and not one had begun secondary replacement; all seven specimens growing P6 and examined for secondary molt had begun replacing their secondaries. The secondaries are organized into an inner and an outer molt series, the first feather of the inner series not always being the same in both wings of a specimen. The feather initiating the inner series could be determined in one or both wings on a total of 12 specimens replacing P6 or P7; it was S6 in two wings, S7 in two, S8 in six, and S9 in nine. In specimens replacing P6 or P7 direction of secondary replacement could be established in seven outer and nine inner series on totals of four and five specimens. In all cases the new or incoming feathers indicated that the secondaries are replaced in an ascending sequence. This is somewhat different from the situation in the Pennant-winged Nightjar for which the Stresemanns (1966: 378) record that "the molt of the inner group [of secondaries] has a descending tendency."

Unfortunately I was unable to check secondary molt in any specimen whose outermost incoming primary was 8 or 9. Four of seven specimens replacing P10 were still growing secondaries, one was growing only S8

and the other three were growing two or three adjacent secondaries at the inner edge of the outer series. These four specimens and evidence from specimens replacing P6 or P7 indicate that the first secondaries replaced are the outermost secondaries of the inner series. Rarely one or more of the innermost secondaries of the outer molt series (i.e. S5 through S8) was unusually worn (e.g. S5 in MCZ 100757), suggesting that it had missed a molt. Specimens often showed some of the innermost secondaries of the inner series (i.e. S10 through S12) in a very worn condition (e.g. CU 12728, LSU 13346, UOMZ 3868). Apparently the innermost secondaries of the inner molt series miss molts much more frequently than do the innermost feathers of the outer series, despite the fact that the secondary molt starts in the inner series.

MOLT OF RECTRICES. Only 8 of over 500 adult and subadult Chucks examined were found to be replacing any of their rectrices, thus the following generalizations about replacement of these feathers can only be considered tentative. Six specimens growing P6 had not begun replacement of the rectrices, and only one (UMOZ 3022 ♂) of eight specimens growing P7 had begun rectrix replacement. As R1 and R2 (numbered from inside out) were fully replaced in this bird (see following tabulation), its tail molt must have begun at least when P6 was growing. I know of only one Chuck taken while P9 was growing (GMS 12195 ♀), and P9 was not yet breaking its sheath in this specimen; all of this bird's rectrices were between about $\frac{1}{4}$ and $\frac{3}{8}$ of their full length (see following tabulation). On the basis of these two specimens it appears that molt of the rectrices is initiated somewhere between the replacement of P6 and P8, and the specimen replacing P9 suggests that some Chucks lose all their tail feathers while P8 is being replaced. The infrequent occurrence of molt of the rectrices in specimens replacing P6 or P7 also suggests a rapid replacement of the rectrices while P8 is being replaced. Molt of the rectrices is probably completed in most birds by the time P10 is full grown or shortly thereafter. Of the 8 specimens growing P10 that could be scored for rectrix molt, 2 had completed the molt, 3 were still growing some of R3 through R5, and 2 apparently had not yet lost either of their 5th rectrices (both these were also growing R4).

Stresemann and Stresemann (1966) note that members of three genera of caprimulgids replace their rectrices in a 1-2-3-5-4 sequence. My eight specimens showed no consistent sequence of replacement, other than a tendency to replace R1 and R2 first and R4 last. Possibly the Chucks' apparent tendency to lose their rectrices nearly simultaneously has obliterated a strict sequence of rectrix replacement. Because of the inconsistency in the sequence of replacement shown by these eight speci-

mens, I have summarized my data on their rectrix replacement in the following tabulation:

FSM 372 ♀: R1 through R4 new, left R5 old, right R5 missing.

FSM 8609 ♂: R1 and R2 new, R3 almost full, R4 about half grown, R5 apparently new (but no flakes of sheathing attracted to the rachises at or near their insertion).

GMS 12195 ♂: All incoming. R1 93 mm, R2 91 mm, left R3 68 mm, right R3 69 mm, left R4 about 31 mm, right R4 about 25 mm, left R5 78 mm, right R5 80 mm. My measurements for the shortest and longest rectrices of this specimen are shorter than those Sutton (1969) published for this specimen. Despite this discrepancy the above measurements indicate the relative length of this bird's 10 rectrices.

KU 16778 ♂: R1, R2, and R3 new, R4 almost full, R5 apparently new.

MCZ 243772 ♀: R1 and R2 new, R3 almost full, R4 about half grown, R5 almost full and about the same length as R3.

UM-MGV 3553 ♀: R1, R2, and R3 new, R4 almost full, R5 new.

UOMZ 3022 ♂: R1 and R2 new, left R3 and R4 about equal, both entirely ensheathed, R5 old.

USF-GEN 92 ♀: R1 and R2 new, R3 almost full, R4 about $\frac{3}{4}$ grown, R5 apparently old (no flakes of sheathing attached to the rachises at or near their insertion).

MOLT OF BODY FEATHERS.—Most of the specimens handled were checked for body molt on the crown, upper back, and ventral surfaces. The sequence of replacement of the body feathers was not worked out. None of seven specimens replacing P6 had begun body molt. Only 4 of 10 specimens replacing P7 had begun replacement of their body feathers, and 3 of these had just begun this replacement. Of the 8 specimens that were replacing P10, 2 had completed the body molt and 6 were still molting, 5 of these being in heavy molt. Sutton (1969) suggests for his specimen that was growing P9 (GMS 12195) that the rictal bristles were lost simultaneously. I have examined only a few specimens that were replacing these feathers, but in each of these all the rictal bristles were less than full length and sheathed at their bases. Apparently these highly specialized feathers are always molted about simultaneously between the replacement of P7 and P9. Sutton (1969) published a photograph of his specimen that illustrates the sheathing at the bases of most of its right rictal bristles.

The preceding data indicate that body molt begins with the replacement of P7 or, probably more frequently P8, and is often not complete upon replacement of P10. The extent of replacement of the body feathers seems to vary considerably as mentioned above. Adult Chucks usually show varying numbers of worn body feathers that apparently have been carried for more than 1, and, in rare cases of extreme wear, perhaps for 2 or more years. Chucks are probably often replacing body feathers after P10 is fully grown, and one might suppose that the complete replacement of the body feathers depends upon a continuum of fall twilights suitable for feeding. On occasional nonmolting specimens (e.g. CU 23138; CU

3625) as many as a fourth or fifth of the contour feathers are very worn, indicating the degree to which the body molt may be incomplete in a given season.

Summary of molt in adults.—The annual molt begins with the loss of P1 and proceeds from P1 to P6 or P7 before molt is evident in any of the other tracts. At about the time the 6th or 7th primaries are dropped, secondary replacement begins at two loci in the secondary series. The meager information on replacement of rectrices indicates that these feathers are lost in some birds, if not simultaneously, at least in quick succession during the time that P8 is being replaced. The body molt also appears to start when P8 is lost, and it is frequently completed some time after P10 is fully grown. The rectal bristles appear to be replaced simultaneously while P8 is growing.

In general the molt is leisurely, and it involves only the primaries until the 6th or 7th primaries are lost. Between the loss of P6 and P8 the intensity of the molt is increased markedly by the initiation of feather replacement in all of the other major groups of feathers. The probable significance of this pattern of progression is discussed below. The degree to which the body molt and, to a lesser extent, the secondary molt is complete in any one season may depend upon the intensity of such proximate factors as inclement weather conditions that force the birds to start the southward migration. Chucks probably rarely leave the breeding grounds until the primary molt is terminated, and in northern latitudes the completion of the primary molt may well be an important factor retarding the time of fall departure. The latest specimen record from Maryland (David Bridge, MS) and the two latest specimen records from Kansas are all provided by birds that were still growing P10. All were taken in September.

Obviously it would be difficult to prove that birds do not begin migration before completing the annual molt, but of seven specimens taken in Mexico (where Chucks do not breed) in August, September, and October, only one was molting. This bird (KU 39978) was taken on 1 September 1961 in Tamaulipas, and its left and right P9 and left P10 were respectively about 8 and 25 mm less than full length (right P10 was apparently lost in preparation). It showed no incoming body feathers or secondaries, though some of the body feathers and the 12th secondaries had not been replaced. It is interesting that the molt of the body feathers and secondaries had apparently been totally arrested in this bird.

The fact that no one, to the best of my knowledge, has taken a Chuck in which 8 is the outermost growing primary must be emphasized. It seems startling to suggest that the molt of an aerial forager might result in temporary flightlessness, but the absence of specimens replacing P8

must surely be the result of more than the general inactivity of both collectors and molting birds in late summer. The only known specimen replacing P9 and the several replacing P10 suggest that at least some Chucks lose their rectrices simultaneously. This loss apparently occurs with the replacement of P8. The secondary molt is well underway when P8 is growing, and the limited available data show some birds growing two or three adjacent secondaries in a series at once. These data and the demonstrated habit of growing two or three primaries at once suggest that some Chucks have trouble flying during the late stages of the molt. At this time these birds would be missing much or all of their tail, the equivalent surface area of about two primaries per wing (these the longest in the wing), and the equivalent surface area of approximately four secondaries per wing. Although Chucks in this shabby condition probably could fly, their ability to catch aerial prey might be rather severely impaired. Furthermore the rictal bristles, which are probably of considerable importance in catching airborne prey, are apparently lost simultaneously when P8 is being replaced. At this stage of their molt Chucks may be dependent in large part upon food they catch by scuttling about on the ground. In this regard Marion Jenkinson and Robert Mengel tell me that they have often seen Chucks move rather rapidly about on foot and pick up objects (mostly pebbles, Jenkinson and Mengel, 1970), and think they could feed well on the ground. If Chucks are either temporarily flightless or so incompetent in flight that they obtain most of their food from the ground at this stage of their molt, the simultaneous loss of the rictal bristles probably has the double advantage of making it easier to pick up prey from the ground and of insuring a complete set of these specialized feathers, without gaps, when Chucks are again catching aerial prey.

SCHEDULE ON THE BREEDING GROUNDS

This section attempts to present a general picture of the schedule of events for the Chuck-will's-widow on its breeding grounds. Specifically, variations in the time of arrival, the time spent in reproductive activities, the timing of the molt, and the time of departure are considered with reference to latitude. Altitudinal variation in the range of the Chuck-will's-widow is relatively small (from sea level to about 1,500 feet), and almost all of my data came from localities below 800 feet elevation. Within its range the length of the summer season and, concomitantly, the time during which flying insects are available in sufficient numbers to maintain an aerial forager's activities are almost certainly more closely related to latitude than to any other easily measured geographic variable.

Simple linear regression has been used to relate the timing of events

on the breeding grounds to latitude. Comparisons of the regression lines for each of the four summer events listed above enables one to ascertain relative differences in their timing at different latitudes. Furthermore, without the use of the regression analysis, it would not have been possible to ascertain the time budgeted to these events at any one locality, because adequate samples of arrival, egg, molt, and departure dates do not exist for any one locality. In each of the following presentations of regression statistics, I have given the percentage of variation in the timing of an event explained by its regression on latitude. The magnitude of these percentages is inversely proportional to the scatter of points around the regression lines (none of these regressions showed any evidence of curvilinearity). Thus if all the variation in the dependent variable, Y , can be accounted for by variation in the independent variable, X , the points around the regression line would show no scatter, and 100 per cent of the variation in Y would be explained by its regression on X . Sokal and Rohlf (1969: 421, 651) show the breakdown of regression variance components from which these percentages were calculated.

It should be safe to assume that the following regression lines are reasonably good general indicators of the relative timing of events in different local populations. They are, however, poorer indicators of the absolute time at which these events occur at any particular locality because of local factors unexplained by latitude. In the sample of arrival dates, for example, it was evident that birds arrived at coastal stations earlier than at inland localities on the same latitude, suggesting the rather obvious probability that local climate and other factors such as migratory pathways are more critical than latitude to which the birds are more or less indifferent except as it affects climate.

Spring arrival.—Almost all of the dates included in the regression of arrival dates on latitude (Figure 2) were taken from the distribution file at the Patuxent Wildlife Refuge. Only localities for which 3 or more years of dates were available were included in the analysis, and no dates were included from localities south of 28° N in Florida because Chucks winter in fair numbers south of this latitude on the Florida peninsula. All the dates used in this regression were reports of first arrival even though some observers also listed the date on which Chucks became common at a locality. Certainly the date on which the majority of the population has arrived is the time of most biological importance; first arrival dates were used only because there were so many more of them. Where both dates were available, birds generally became common at a station within a week of their first noted appearance.

The regression of arrival dates on latitude is based on 32 samples from 28.55° N to 39.18° N, including 308 observations. The slope of this line

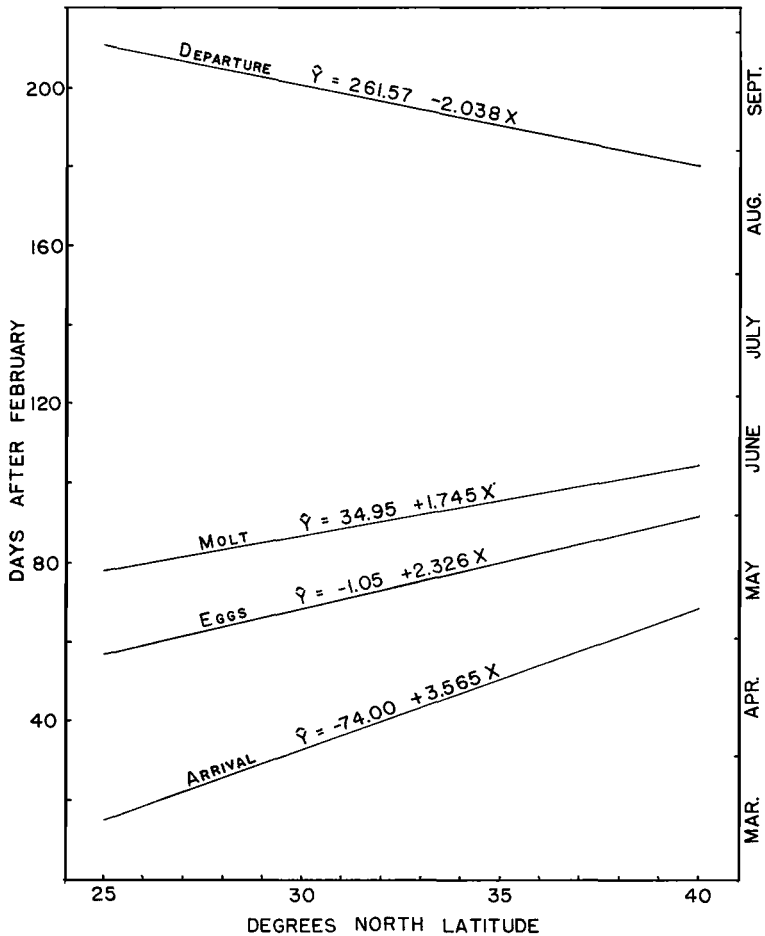


Figure 2. Regressions of dates of first arrival, egg-dates, dates of replacement of P1 through P4, and dates of last fall observation on latitude. See text for reliability of these lines. Day one on the ordinate is 1 March.

differs significantly from 0 ($P < 0.001$), and the 95 per cent confidence limits of the slope are +2.376 and +4.754. This regression explains 55 per cent of the variation in arrival dates. At least a moderate amount of the unexplained variation is probably due to the above-mentioned tendency of Chucks to move northward earlier along the coast than in inland regions.

As mentioned above, the time of greatest interest is not the arrival of the first individual, but the time when the majority of the population has arrived. This regression line would probably represent the arrival

of the majority of the population if it were raised 5 to 7 days. Also the supposed arrival of the Chuck-will's-widow is usually heralded by a singing male; thus this regression essentially must summarize the presumed arrival of the males on the breeding grounds. According to Sprunt (*in* Bent, 1940: 148), the males always arrive first, followed in a few days by the females.

Egg-dates.—Egg-dates were obtained from egg collections, the literature, records in the distribution file at Patuxent Wildlife Refuge, notes from private individuals, and files of nest records cards. Obvious duplications were eliminated from the sample. Few dates could be taken from state bird books because the authors typically list only extreme dates. As information accompanying most records of eggs was insufficient for estimation of the date of clutch completion, no extrapolations were made. For cases where the fate of the eggs was followed for some time, the date on which the eggs were first found was used in the analysis. The incubation period for Chucks is around 20 days (Hoyt, 1953); thus, there is room for a considerable amount of unexplained variation resulting from the use of egg-dates not corrected to some standard (such as date of clutch completion), and the unexplained variation may be expected to be high.

The regression of egg-dates on latitude (Figure 2) is based on 80 samples from 25.78° N to 39.05° N, including 264 dates. The slope of this line is significantly different from 0 ($P < 0.001$), and the 95 per cent confidence limits of the slope are +1.62 and +3.03. As predicted above, this regression explains a rather low 35.6 per cent of the variation in egg-dates.

For comparisons of the relative scheduling of events on the breeding grounds it would be desirable for the regression of egg-dates on latitude to indicate the average completion of first clutches. Assuming an equal probability of finding nests throughout incubation, this line would be moved to lie about 10 days earlier in the season to indicate the average completion of the sample of clutches used. However if nests frequently failed during incubation and if little or no renesting occurred, the average day on which one would expect to find eggs would tend to be earlier than the 10th day of the incubation period because more nests would exist in the first half of the incubation period than in the latter half. On the other hand, if Chucks regularly produce replacement clutches when their first eggs are lost, the average day on which one would expect to find eggs would tend to be more than 10 days after the first clutches were laid. In southern latitudes Chucks almost certainly have time for replacement clutches, and have been suspected of laying them. C. E. Doe (field notes) suspected that two sets taken 26 days apart (UF 89477 and UF 89478) were laid by the same pair; the second of these two sets was taken near the earlier nest and the egg markings were similar (*vide* Dinsmore, letter

of 6 August 1968). Toward the northern edge of the Chuck's range the time available for replacement clutches must be progressively reduced until, possibly at the northern edge of their range, replacement clutches cannot be laid. Thus the regression of egg-dates on latitude probably should be depressed more than 10 days in the south, and a little less than 10 days at the northern edge of the breeding range to represent the average initiation of breeding, as measured by the completion of first clutches.

An implicit assumption in the regression of egg-dates on latitude is that the Chuck does not normally raise two broods. If this assumption does not hold, a large sample of egg-dates from any one locality would deviate strongly from a normal distribution and one of the assumptions of the regression analysis would not be met. The literature contains no direct information on the number of broods Chucks raise. The European Nightjar (*Caprimulgus europæus*) is typically double-brooded in England (Lack, 1930, 1931), and the Common Nighthawk occasionally raises two broods (Weller, 1958).

As at least the two best-studied caprimulgids are known to raise two broods, albeit with very different frequency, it seemed desirable to plot a histogram of egg-dates for a single locality for the Chuck-will's-widow. Such plots of egg-dates throughout the nesting season are known to be multimoded, or at least more flattened than normal (platykurtic), for species that typically raise more than one brood per season (Woolfenden and Rohwer, 1969, Figure 3 and Figure 10). Unfortunately no large sample of egg-dates from one locality exists for the Chuck; but 139 egg-dates were available from the entire Florida peninsula. A separate regression on latitude was calculated for these dates yielding a line described by the equation $Y = -101.49 + 5.89X$. The slope of this line is significantly different from 0 ($P < 0.05$), and its 95 per cent confidence limits were +1.58 and +10.21.

Using this regression equation, the 139 Florida egg-dates were adjusted to a single latitude. The distribution of this corrected sample was then tested for kurtosis (or peakedness) using the g_2 statistic (Sokal and Rohlf, 1969: 112–118). g_2 is 0 for normal distributions, negative for platykurtic distributions, and positive for leptokurtic (or peaked) distributions. A normal or leptokurtic distribution should be strong evidence for single broodedness because a species that is regularly double brooded should show a platykurtic or multimodal distribution of egg-dates.

The 139 egg-dates from localities south of 30° N on the Florida peninsula were corrected to 27.96° N using the peninsular regression equation. The statistic for skewness, g_1 (Sokal and Rohlf, *ibid.*), showed the distribution to be skewed right ($P < 0.05$). As g_2 was significantly positive ($P < 0.05$),

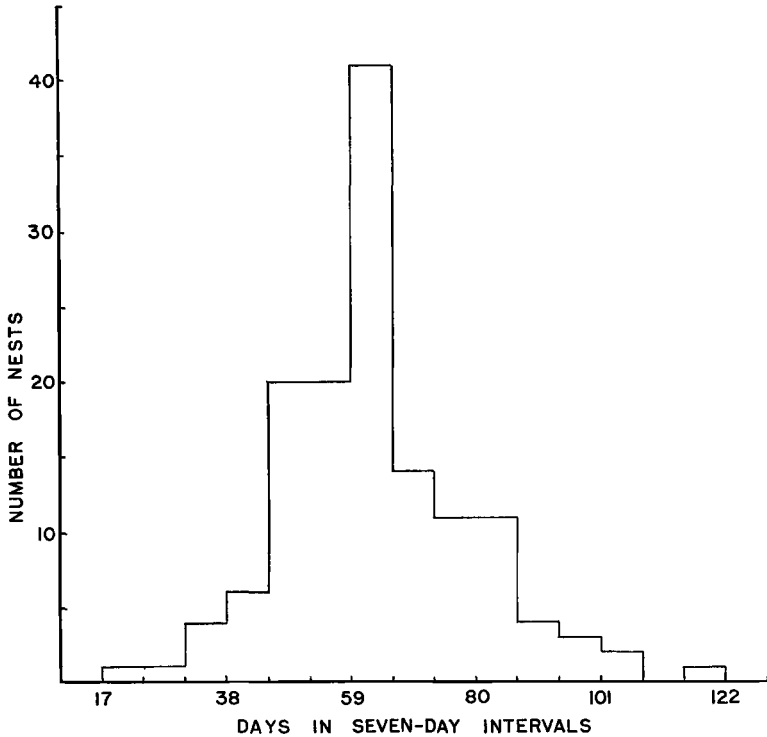


Figure 3. Histogram of 139 egg-dates from the Florida peninsula. All dates were adjusted to 27.96° N using the regression equation for egg-dates on latitude for the peninsula. The abscissa begins at 10 March.

indicating a pointed distribution (Figure 3), Chuck-will's-widows may be assumed to be single brooded. The slight skew to the right probably is caused by renestings after eggs are lost, which might be expected at this extreme southern locality.

Inception of the molt.—For the regression of the inception of molt on latitude (Figure 2), dates were used from all specimens molting P1 through P4. This gave a reasonably large number of dates with a fairly even north-south distribution of localities.

As separate regressions for the sex classes of adults were not significantly different in either their slope ($P > 0.05$) or placement ($P > 0.05$), sexes were lumped in the following analyses. Since adults and subadults can be separated in specimens molting P1 through P4, separate regressions were also calculated for these age classes (two specimens of uncertain age were excluded) (Figure 4). As there is no significant difference in either the slope ($P > 0.05$) or placement ($P > 0.05$) of these lines, there is no

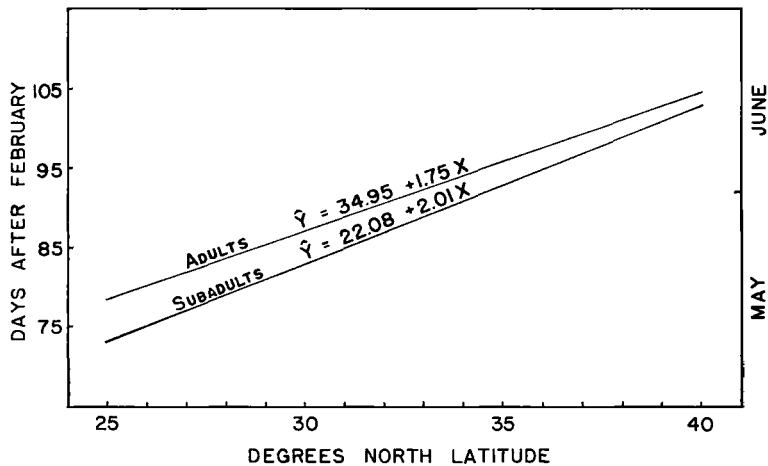


Figure 4. Regressions of date of replacement of P1 through P4 on latitude for adult and subadult Chuck-will's-widows. For reliability of the lines and other relevant data see text.

statistical reason not to lump these samples; but until it is known whether or not subadults breed, it seems unsound biologically to do so. Therefore the line shown in Figure 2 is based only on the sample of adult birds.

The regression of adults molting P1 through P4 (Figures 2 and 4) is based on 24 samples from 25.82° N to 38.79° N, including 41 dates. The slope of this line differs significantly from 0 ($P < 0.01$) and the 95 per cent confidence limits of the slope are +0.493 and +2.998. This regression explains a rather low 27.5 per cent of the variation in molt dates. Part of the unexplained variation probably can be accounted for by the increased variation in my sample caused by using birds replacing any of P1 through P4 rather than only birds replacing P1. Also, if Chucks must be beyond some point in their reproductive cycle to begin the molt, the variance in the initiation of last clutches is automatically added to the natural variation in the inception of the molt.

The regression of subadults molting any of P1 through P4 (Figure 4) is based on 9 samples ranging from 25.91° N to 37.15° N, including 10 dates. Its slope also differs significantly from 0 ($P < 0.01$) and the 95 per cent confidence limits of the slope are +0.967 and +3.045. Regression on latitude explains 73.9 per cent of the variation in these molt dates. The greatly reduced scatter of points around the regression line for subadults as compared to adults indicates a much greater synchrony among subadults in the timing of their molt; this synchrony suggests that they do not breed.

For comparison of the initiation of the molt with the initiation of breeding, the regression line for molt should be depressed because it is based on dates of specimens whose outermost growing primary was any of P1 through P4. The magnitude of this depression can be estimated only roughly, because no information is available on the rate of primary growth in the species. White-throated Swifts (*Aeronautes saxatalis*) require approximately 12 days to replace completely any one of their first seven primaries (Rohwer, MS). Even though Chucks are frequently replacing two or three adjacent primaries at once, I would guess that this line should be lowered a minimum of 10 to 15 days.

Departure.—The time of fall departure is difficult to establish for many migratory species because pertinent data typically consist of dates of last observation. Such dates can give an erroneously late impression of the average departure time if the bulk of the population typically leaves before an observable number of stragglers leave, or an erroneously early impression of the average departure time if the birds are not seen with any regularity shortly before their actual departure. This latter problem is undoubtedly severe for the Chuck-will's-widow, a secretive, nocturnal species, which is rarely vocal in late summer, and which inhabits largish wood lots that seldom are visited by bird students in late summer.

All my dates of last observation were obtained from the distribution files at Patuxent Wildlife Refuge. Curiously enough, about a third of these dates were for the months of May, June, or July. Certainly such early dates have nothing to do with the beginning of southward migration. To obtain an index of when Chucks might begin leaving the breeding grounds, I have assembled the earliest fall arrival dates that I could find for various points along the migration route and in the wintering grounds (Table 2). It is apparent from these dates that at least some Chucks leave their breeding grounds in late August, but I have no evidence suggesting that they ever leave any earlier than mid-August.

To obtain an index of when Chucks are typically last found on their breeding grounds I have arbitrarily included in this regression only dates recorded after 15 August. Obviously this sample is not random, but it seemed desirable to have a regression line relating the approximate time of fall departure to latitude for comparison with the other lines. The position of this line probably could only be too early in the season. No dates reported from south of 28° N on the Florida peninsula were included in the sample as Chucks regularly winter south of this latitude on the peninsula.

The regression for departure dates on latitude (Figure 2) is based on 32 samples ranging from 28.16° N to 38.33° N, including 79 observations. The slope of this line is significantly different from 0 ($P < 0.05$); 95 per

TABLE 2
SOME EARLY FALL ARRIVAL DATES FOR THE CHUCK-WILL'S-WIDOW

| Date | Locality | Source or specimen number |
|---------------|------------------------------|--|
| 22 Aug. 1966 | Dry Tortugas, Florida | W. B. Robertson (letter, 26 Dec. 1968) |
| 22 Aug. 1948 | Near Teziutlan, Veracruz | FMNH 187127 ♀ s ¹ |
| 28 Aug. 1948 | West Indies | Bond (1956) |
| 1 Sept. 1961 | San Fernando, Tamaulipas | KU 39978 ♂ ad. |
| 4 Sept. 1898 | Port of Sagua, Cuba | ANSP 35162 ♀ s ¹ |
| 7 Sept. 1961 | Villa Mainero, Tamaulipas | KU 39979 ♀ s ¹ |
| 11 Sept. 1925 | Near San Miguel, El Salvador | FMNH 111330 ♀ s ¹ |
| 12 Sept. 1907 | Matagalpa, Nicaragua | AMNH 102442 ♂ ad. |
| 13 Sept. 1930 | Matamoros, Tamaulipas | UMMZ 164037 ♀ ad. |

¹ s indicates presumed subadult.

cent confidence limits for the slope are -3.251 and -0.825 . This regression explains 28.2 per cent of the variation in the dates of last observation. Undoubtedly a considerable amount of the unexplained variation in this sample is caused by the problem mentioned above of using dates of last observation as an index of departure.

Interpretation.—As a basis for an orderly consideration of the Chuck-will's-widow's summer schedule, a new figure (Figure 5) was drawn showing the positions of the first three lines of Figure 2 adjusted to provide an estimation of the arrival of the majority of the population, the average completion of first clutches, and the average initiation of annual molt. Rationales for so moving these lines were presented above. An additional line in Figure 5 represents the average time that young should be gaining independence from their parents. This line is placed 40 days above the original regression of egg-dates on latitude. Its placement is based on a 20-day incubation period (Hoyt, 1953; Nunley, 1960), a 16-day period for young to fledge (Wilson, 1959), and an additional hypothetical 14-day period during which flying young are dependent upon their parents. The latter period is unknown for Chucks and 14 days is used because is is the approximate time that fledged Common Nighthawks are dependent upon their parents (Bent, 1940: 220–221; Weller, 1958). Note that the line indicating the average time young should be gaining independence from their parents is not placed 50 days above the line estimating the average completion of first clutches. This is because it is meant to depict not the average time that young of first clutches are becoming independent, but the average time that young of all clutches, replacements included, are becoming independent. The original regression of egg-dates should be an average of the midpoints of the incubation periods of all

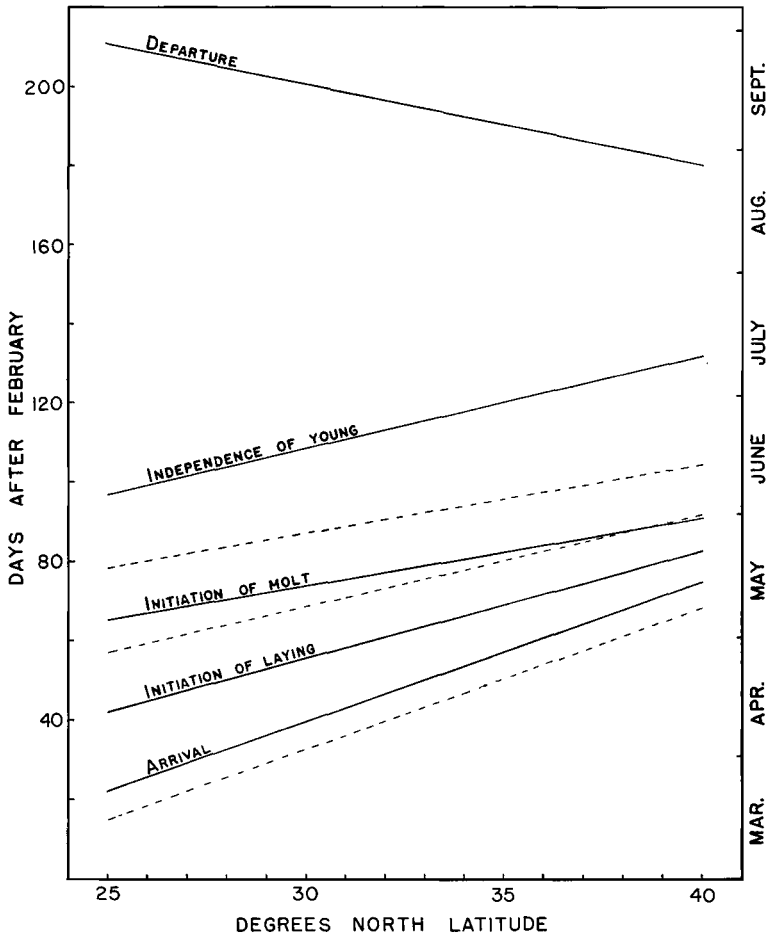


Figure 5. Lines estimating the average dates of (1) the arrival of the majority of the population, (2) the initiation of laying, (3) the initiation of the molt, (4) the independence of young, and (5) the departure of the population related to latitude. Placement and reliability of these lines are discussed in the text. The three dashed lines are the original regressions of arrival, egg, and molt dates on latitude as given in Figure 2. Day one on the ordinate is 1 March.

clutches. Thus a line indicating the average time that young of all successful nestings become independent probably lies about 40 days above the original regression of egg-dates on latitude (10 days to complete incubation plus 16 days to fly plus an additional 14 days dependence on adults). No change has been made in the placement of the line summarizing departure dates.

northern latitudes, it probably continues until birds begin the southward migration. One might roughly estimate from the temporal space between the line summarizing the initiation of the molt and the line summarizing departure dates that Chucks require from 3 to 4 months to complete the annual molt.

The insect biomass generally increases markedly throughout the summer. In Kansas the numbers and biomass of diurnal flying insects appear to reach a maximum in late August and early September (Johnston, 1967). Thus many insect-eating aerial foragers that molt on their breeding grounds in the north-temperate zone undergo the annual molt when food is most abundant. From Figure 5 it is evident that Chucks spend in reproductive activities less than the first half of their total time on the breeding grounds. Were it not for the annual molt, Chucks would apparently have ample time to produce two broods. The European Nightjar regularly raises two broods per season in England (Lack, 1930, 1931). Males of this species take over the entire care of the first brood about 10–14 days after hatching while the female lays and incubates the second clutch. Moreover European Nightjars molt on their wintering grounds in Africa.

The rather rapid convergence of all of the regression lines (Figures 2 and 5) as one moves northward implies that the time required to raise young and complete the annual molt may be an important factor limiting the Chuck's northern distribution. Certainly under present climatic conditions, it does not appear that Chucks could exist much, if any, farther north without somehow reducing the time required for these events.

COMPARISONS WITH OTHER AERIAL FORAGERS

Most small to medium-sized north-temperature migratory land birds undergo their postnuptial molt on their breeding grounds before starting south. Almost all the species that postpone either all or part of the postnuptial molt until arriving on the wintering grounds are among the inveterate aerial foragers, the nightjars, swifts, flycatchers, and swallows (see Dwight, 1900: 113, and below). In the context of other aerial foragers the Chuck's postnuptial molt on the breeding grounds seems to merit some discussion. In the following paragraphs all of my information on the geographic location of the molt of North American species has been taken either from Dwight (1900) or Bent (1940, 1942) unless another source is given.

Many North American flycatchers and swallows raise but one brood per season and molt on their wintering grounds. These species appear to be under severe time limitations on their breeding grounds (many range well into Canada and Alaska) and probably are not pertinent to this

discussion because they do not have time to meet more than a single major energetic demand while on their breeding grounds. Of particular pertinence to this discussion are those migratory aerial foragers that molt on their breeding grounds. Were it not for the molt, these species would appear to have ample time to raise an additional brood of young as the annual molt typically requires 2 to 3 months in small to medium-sized land birds (estimates in Stresemann and Stresemann, 1966: 33-34; Miller, 1961). Because a potentially greater number of offspring might be produced by postponing the molt until the arrival on the wintering grounds, a complex of factors must exist strongly countering its postponement. Factors that may counter the postponement of the molt are immediately apparent for some of these species.

Ash-throated and Great Crested flycatchers (*Myiarchus cinerascens* and *M. crinitus*) molt on their breeding grounds and both are hole nesters. Late summer specimens of both of these species are usually severely worn and would be much more worn if they produced two broods. Probably the inefficiency of migrating with a badly abraded plumage is the critical factor dictating their molt on the breeding grounds.

Many populations of a number of North American aerial foragers that molt on their breeding grounds have a rather northern wintering distribution as summarized in the 1957 edition of the A.O.U. Check-List. Among these are the Poor-will (*Phalaenoptilus nuttallii*; Rohwer, MS), Lesser Nighthawk (*Chordeiles acutipennis*), possibly Vaux's Swift (*Chaetura vauxi*), White-throated Swift (Rohwer, MS), Say's Phoebe (*Sayornis saya*), Eastern Phoebe (*S. phoebe*; the Black Phoebe, *S. nigricans*, is largely a resident bird), Tree Swallow (*Iridoprocne bicolor*), and Violet-green Swallow (*Tachycineta thalassina*). Presumably winter food shortages preclude the postponement of the molt until arrival on the wintering grounds in these species. Winter kills, indicative of food shortages, have been recorded for at least three, White-throated Swifts (Hanna, 1917), Eastern Phoebes (McIlhenny, 1940), and Tree Swallows (Christy, 1940).

It is also of interest to note that Poor-wills and White-throated Swifts show adaptations in their molts that apparently enable them to complete the molt at high elevations in the Rocky Mountains. I have recently discovered that at least certain populations of Poor-wills from the Rockies show a step-wise molt of their primaries (Rohwer, MS). Ashmole (1968) has argued most convincingly that stepwise primary molts (see Stresemann and Stresemann, 1966: 21-22) are an adaptation for rapid completion of the molt while maintaining maximum aerodynamic stability. White-throated Swifts in the Rockies show a typical sequence of feather replacement, but initiate their molt early in the breeding cycle apparently to assure its completion before the fall migration. Johnson (1963) has shown

that Hammond's Flycatcher (*Empidonax hammondi*) molts on the breeding grounds, and he correlates this with the fact that Hammond's Flycatcher winters from 3,500 to 8,700 feet in the Central American Highlands while several other empidonaces that molt on the wintering grounds winter below 3,500 feet.

In summary, many aerial forages probably molt on their wintering grounds because time limitations do not allow them to breed and to molt on their breeding grounds. For others compelling circumstances exist, such as plumage wear or relatively northern winter distributions, which make the occurrence of the postnuptial molt on the breeding grounds seem reasonable. For some, however, the occurrence of the molt on the breeding grounds at the apparent expense of the production of an additional brood seems difficult to justify. Among these are the Western Kingbird (*Tyrannus verticalis*) and the Scissor-tailed Flycatcher (*Muscivora forficata*) that probably molt on their breeding grounds, and the Acadian Flycatcher (*Empidonax virescens*) that definitely molts on its breeding grounds (Mengel, 1952; Traylor, 1968). Although some Chucks overwinter in the extreme southern United States, most adults winter in the tropics, therefore their molt on the breeding grounds cannot be explained by a relatively northern winter range.

EVIDENCE FROM THE WINTERING GROUNDS

Fretwell (1969) recently offered a seemingly impeccable explanation for reproductive rates that are lower than the apparent capacity to produce independent young in a single breeding season. In brief, if any sort of hierarchy exists in a population that regulates the exploitation of a limiting resource, the least dominant individuals will be the first to be eliminated in times of stress. Given a dominance hierarchy any reproductive effort, such as double-broodedness, that produces more young than can be carried through the annual minimum in food supplies, is wasted. The later fledged young are subordinate to those fledged earlier, and will be the first to be eliminated from the population.

Providing my assumption that Chuck-will's-widows are territorial in winter is true, Fretwell's hypothesis seems to explain the occurrence of the molt on the breeding grounds and the production of but one brood per season. Chucks winter in extreme southern United States, Central America, Columbia, and most of the West Indies, on a land surface about $\frac{1}{2}$ the size of their breeding range. Intraspecific competition may be intense in this small wintering range, and interspecific competition with the closely related Rufous Nightjar (*Caprimulgus rufus*), common in Central America and the Antilles, and other tropical and wintering North

American nightjars also may be important. In an attempt to assess the relative ability of adult and subadult Chucks to survive the winter, I have calculated the number of subadults per 100 adults in fall and spring collections. For the fall sample the only specimens considered were taken in September or October when both adults and subadults of the previous year have completed the molt. This sample included 37 subadults and 20 adults, or 185 subadults/100 adults. As Chucks lay but two eggs per clutch and raise only one brood per season, the sample may be biased in favor of subadults. On the other hand the major mortality of adults may occur in late summer when, possibly, they are flightless (see earlier section), and the predominance of subadults in fall collections may not represent sampling error.

For the spring sample I used only specimens taken in April and May to avoid the possibility of including in the subadult category birds fledged in different seasons. This sample contained 134 adult males and 64 presumed adult females. Males were 2.1 times as conspicuous to collectors as females in this sample, presumably a result, not of unbalanced sex ratios, but of their persistent territorial singing. Assuming that subadult males do not sing and are generally about as inconspicuous as females, I have adjusted the sample of 26 subadult males by multiplying it by 2.1, giving 55 subadult males. The spring sample included 30 presumed subadult females. Using the adjusted total for the spring sample of 85 subadults and 198 adults, the ratio is 43 subadults per 100 adults.

With these figures, the mortality rate of subadults over the winter can be estimated as $185/43 = 4.32$ times that for adults. Even if one chooses to assume that the fall ratio of adults to subadults should be approximately 1 : 1, there is still a considerably greater mortality in subadults, $100/43 = 2.33$.

This excess mortality of subadults is undoubtedly a function in part of their use of different wintering grounds. Its magnitude also suggests that more young are produced from first clutches than can overwinter on the present area of the wintering grounds. If the wintering grounds cannot be expanded, reproductive efforts spent on the production of second broods, and perhaps even late replacement clutches, would solely decrease the probability of adults surviving while adding nothing to the number of potential breeding offspring produced.

If more young are produced in a single brood than can survive on the wintering grounds, the molt on the breeding grounds seems entirely reasonable. But why should it occur during the late summer peak in numbers of flying insects (Johnston, 1967, Figure 1), while the energetically more demanding breeding activities take place in spring and early

TABLE 3
GEOGRAPHIC DISTRIBUTION OF ADULT AND SUBADULT CHUCK-WILL'S-WIDOW SPECIMENS
TAKEN IN OCTOBER THROUGH FEBRUARY

| | Central and South America | Southern United States | Cuba | Greater Antilles exclusive of Cuba | Totals |
|--------------------|---------------------------------|------------------------------|------|---|--------|
| Subadults | 20 | 14 | 12 | 2 | 48 |
| Adults | 9 | 6 | 10 | 22 | 47 |
| Totals | 29 | 20 | 22 | 24 | 95 |
| Per cent subadults | 69.0 | 70.0 | 54.5 | 9.1 | 50.5 |

summer when flying insects are less plentiful? For species that severely abrade their plumage during the breeding season, the advantage of migrating and wintering in a fresh plumage is undoubtedly an important factor causing the molt to occur after breeding. In Chucks, however, plumage wear associated with reproductive events is not discernable.

Fretwell's (1969) dominance hypothesis also provides the best explanation of the occurrence of the molt after rather than before reproductive events. As plumage wear is unimportant, the postreproductive molt is apparently dictated by the better survival of earlier fledged young that will occupy more favorable positions in the dominance hierarchy. The implication is that no causal relationship exists between the synchrony of the annual molt and the late summer maximum in food supplies. Presumably this synchrony is only a consequence of selection favoring the earliest fledged young. A similar interpretation also might explain the occurrence of the annual molt in the Steller's Jays of the Queen Charlotte Islands at the presumed peak in food abundance (Pitelka, 1958).

If adults have always been much superior to young in winter survival, the remarkable segregation of adults and young on the wintering grounds seems susceptible to interpretation. The winter quarters were divided into four geographically coherent subsets from which samples of approximately equal size were available (Table 3). In an original classification, these data were also broken down into monthly intervals. G-tests of independence (Sokal and Rohlf, 1969) showed that months and localities ($P \approx 0.20$) and months and age classes ($P \approx 0.20$) were independent. There was, however, a highly significant dependency between age class and locality ($P < 0.001$). Central and South America, the southern United States, and Cuba form a statistically homogeneous subset of localities, indicating that the heterogeneity among localities is caused largely by the striking difference between the ratio of adults and

subadults in these localities collectively versus the ratio in the Greater Antilles exclusive of Cuba.

The preference shown by adults to winter in the Greater Antilles rather than in Central and South America is probably due to the risk of long overwater migrations, although the greater abundance of potential competitors in Central and South America compared with the Antilles may also be important. All of the Greater Antilles can be reached by island hops that require no more, and typically much less, than 200-mile flights over water. Although some of the Chucks wintering in Central and South America undoubtedly funnel through northern Mexico (Friedmann, et al., 1950; and several other specimens, Rohwer, MS), many more probably fly directly across the Gulf of Mexico (Lowery, 1945, 1946). In a fascinating account of three birds on shipboard off the Atlantic Coast, Thayer (1899) gives a fine description of the probable death of a migrating Chuck caught at sea by cold, foggy weather. The southern United States is undoubtedly a marginal wintering area because of rather frequent periods of prolonged cold that sometime result in major kills of Chucks and other aerial foragers (Weber, 1940).

There is, thus, good reason to believe that selection opposes Chucks wintering anywhere except in the Greater Antilles. This selection presumably applies to both adults and subadults, and were it not for the small size of these islands one might expect all Chucks that do not migrate through Central America to have evolved an Antillean wintering habitus. Undoubtedly enough adults exist to fill up the Antilles, therefore subadults that attempt to winter there must stand a very small chance of surviving because of their inferior dominance status. Selection would then favor subadults wintering in the climatically less stable areas such as the southern United States. The end result is that the most favorable wintering area is occupied almost entirely by adults, thus giving the lowest mortality rate to the age class with the greatest reproductive potential. Furthermore if subadults do not attempt to breed, as suggested by the small unexplained variance in their regression of primary molt on latitude as compared with adults, they should be able to arrive as yearlings on the tropical wintering grounds for their first winter earlier than the older and more experienced adults. This should give them a certain squatters' rights advantage over the adults and help integrate them into the older portion of the adult population.

ACKNOWLEDGMENTS

I thank the following persons for lending specimens maintained at their institutions; an abbreviation is given for each institution having a specimen that was individually cited in this paper: Dean Amadon, American Museum of Natural History (AMNH);

N. Philip Ashmole, Peabody Museum of Natural History, Yale University; Oliver L. Austin, Jr., Florida State Museum at the University of Florida (FSM); Jon C. Barlow, Royal Ontario Museum; Emmet R. Blake, Field Museum of Natural History (FMNH); James Bond, Academy of Natural Sciences of Philadelphia (ANSP); C. L. Douglas, Texas Memorial Museum, University of Texas; Douglas A. James, Department of Zoology, University of Arkansas; Ned K. Johnson, University of California Museum of Vertebrate Zoology; Richard F. Johnston, University of Kansas Museum of Natural History (KU); George H. Lowery, Jr., Louisiana State University Museum of Zoology (LSU); Y. J. McGaha, University of Mississippi (see below under Vaiden); Oscar T. Owre, Department of Zoology, University of Miami; Kenneth C. Parkes, Carnegie Museum; Raymond A. Paynter, Jr., Museum of Comparative Zoology, Harvard University (MCZ); Robert W. Storer, University of Michigan Museum of Zoology (UMMZ); George M. Sutton, University of Oklahoma Museum of Zoology (UOMZ); Milton B. Trautman, Ohio State Museum (OSM); A. R. Weisbrod, Cornell University (CU); Glen E. Woolfenden, University of South Florida (specimens cited by USF followed by collector's initials and field number); and Richard L. Zusi, United States National Museum. G. M. Sutton (GMS) and M. Gordon Vaiden kindly lent me specimens from their personal collections; Vaiden has subsequently given his specimens to the University of Mississippi, thus they are cited by UM-MGV followed by Vaiden's field number.

I am very grateful to Richard Zusi, Gary Schnell, and James Dinsmore for extracting egg dates for me from the collections at the U. S. National Museum, the American Museum of Natural History, and the University of Florida. Thanks are also due to George Miksch Sutton, M. Gordon Vaiden, David F. Parmelee, and Marion and Robert Mengel for providing egg dates from their personal or institutional files. Milton B. Trautman very kindly sent me information on the state of incubation for the set of eggs and molting female parent that he collected in Ohio. My thanks are also extended to William B. Robertson for sending me migration dates from south Florida and the Dry Tortugas, and to Ned K. Johnson for information concerning a specimen in the Museum of Vertebrate Zoology.

I am indebted to Robert S. Hoffmann, Robert M. Mengel, David M. Niles, and Gary D. Schnell for many helpful comments on an earlier version of this paper. The detailed comments by Dr. Mengel have increased considerably the quality of this work, the progress of which he facilitated in various other ways. Special thanks are due to my wife Brigitte who, with utmost sympathy, helped measure specimens, typed and retyped the manuscript, and made the final versions of the figures.

Two National Science Foundation travel grants in Systematic and Evolutionary Biology (NSF GB-4446X) enabled me to visit several large museums to examine specimens. The principal investigator for this grant at the University of Kansas was George W. Byers. I am grateful to the University of Kansas Computation Center for the computer time required to do the computations for most of the statistics presented in this paper.

SUMMARY

The first part of this paper treats in some detail the sequence of molts and plumages of the Chuck-will's-widow. No sexual dimorphism was found in birds clothed in the natal down or the light ochreous-buff juvenal plumage. The molt into the first winter plumage probably begins before young birds can fly and results in the replacement of all of the lightly

colored body feathers, but not certain dark feathers including the rectrices and remiges. No winter or spring molt occurs in either adults or young of the year, thus young birds wear the first winter plumage until they are about a year old. Males in first winter plumage lack the white areas in the three outermost pairs of rectrices typical of adults and cannot be distinguished from females in the first winter plumage. Both males and females in the first winter plumage can usually be distinguished from older females by their narrower and typically more pointed rectrices, by the lightness of their innermost secondaries, and by the absence of any worn body feathers some of which are usually present in the plumage of adults.

The sequence of replacement of the primaries, secondaries and rectrices is described in considerable detail; body molt is treated in a more general way. The annual molt is initiated by the loss of the first primary and proceeds to the loss of primary six or seven before molt is begun in any other feather tract. At this stage in the replacement of the primaries, the molt is initiated in almost all of the other feather tracts and proceeds rapidly to completion. At about the time the eighth primary is being replaced feather replacement is so intense that some birds may either be flightless or possibly so incompetent in flight that they are dependent largely upon food they catch on the ground.

The second part of this paper relates arrival on the breeding grounds, initiation of laying, initiation of the annual molt, and fall departure to latitude by linear regression analysis. All regression lines converge as one moves north, indicating that the time available in the summer to establish territories, successfully reproduce, and complete the annual molt is a critical limiting factor at the northern edge of the species' range. The positions of these lines indicate that the molt is begun, at least in northern latitudes, while the adults are incubating, and probably continues until about the time of fall departure. It is suggested that the sudden increase in the intensity of the molt at about the time primary seven is being replaced may be correlated with the cessation of parental duties.

Many migratory aerial foragers are known to molt on their wintering grounds, and it is noted that if the Chuck-will's-widow did this, it should have ample time and food resources to raise two successful broods per season that, by virtue of leaving a greater number of offspring, would appear to have a considerable selective advantage. An approximately threefold excess in the mortality of subadults as compared to adults over the winter suggests that Chucks produce more young in a single brood than can survive on the present area of wintering grounds. If this is true, Fretwell's (1969) dominance hypothesis explains the occurrence of the molt on the breeding grounds. The presumed subdominant status of

subadults also makes it possible to explain the evolution of adults occupying the most favorable wintering grounds.

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