THE MOLT OF SCRUB JAYS AND BLUE JAYS IN FLORIDA

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ORNITHOLOGICAL MONOGRAPHS NO. 29
PUBLISHED BY
THE AMERICAN ORNITHOLOGISTS' UNION
WASHINGTON, D.C.
1982

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ORNITHOLOGICAL MONOGRAPHS

This series, published by the American Ornithologists' Union, has been established for major papers too long for inclusion in the Union's journal, *The Auk*. Publication has been made possible through the generosity of the late Mrs. Carll Tucker and the Marcia Brady Tucker Foundation, Inc.

Correspondence concerning manuscripts for publication in the series should be addressed to the Editor, Dr. Mercedes S. Foster, USFWS, National Museum of Natural History, Washington, D.C. 20560.

Copies of *Ornithological Monographs* may be ordered from the Assistant to the Treasurer of the AOU, Glen E. Woolfenden, Department of Biology, University of South Florida, Tampa, Florida 33620. (See price list on back and inside back cover.)

Ornithological Monographs, No. 29, viii + 51 pp.

Editor of AOU Monographs, Mercedes S. Foster

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First received, 22 December 1980; accepted, 7 April 1981; final revision completed, 16 July 1981

Issued January 14, 1982

Price $8.00 prepaid ($6.50 to AOU members)

Library of Congress Catalogue Card Number 81-86487

Printed by the Allen Press, Inc., Lawrence, Kansas 66044

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

Molt and breeding usually have separate schedules in the annual cycles of birds. The most common explanation given is that by staggering these two events birds are subject to less energy stress (Kendeigh 1949; Farner 1964). Reported exceptions include some birds living in tropical climates, where presumably food availability fluctuates less seasonally, and some birds from high latitudes, where apparently for a short time during the year sufficient food exists for the completion of both molt and breeding (Payne 1972).

Missing from most reports on molt-breeding overlap are molt data for individuals whose exact breeding status is known. Because the breeding schedules of populations, and especially populations living in warm climates, can extend far beyond that of an individual in that population, the information on true molt-breeding overlap is far more limited than the literature suggests. Furthermore, if molt begins gradually, then the mere fact that molt overlaps with breeding contributes little information useful to the study of the scheduling of major activities in the annual cycle of birds.

Characteristics of the annual cycles of the two jay species that breed in Florida suggested that detailed knowledge of their molt regimes might contribute to the overall understanding of molt in birds. Scrub Jays (*Aphelocoma coerulescens*) in Florida have a relatively short nesting season, March through June, and usually attempt to produce only one brood of fledglings per year (Woolfenden 1974). In contrast, Blue Jays (*Cyanocitta cristata*) in Florida regularly nest into August, and probably regularly attempt to produce two broods of fledglings per year (Woolfenden and Rohwer 1969). In addition, Florida Scrub Jays are cooperative breeders, and many pairs are assisted by non-breeding helpers (Woolfenden 1974, 1975). Therefore, the population includes some adult individuals that have yet to breed. Finally, these two closely related species exist in populations that breed sympatrically in a subtropical climate where, presumably, food is less scarce in winter than in more temperate regions.

Pitelka's (1945) careful study of pterylography and molt in Scrub Jays provides a firm foundation for our work. Further study of molt in Scrub Jays was justified, however, because few Florida birds were available to Pitelka, and because neither the breeding chronology of that population, nor the fact that it exhibits cooperative breeding with non-breeding helpers was documented at the time. Because of the existence of a banded population, we describe molt for numerous Scrub Jays of known age, sex, and exact breeding status. Our age and breeding information on Blue Jays is less detailed. Remarkably, however, despite extensive banding at many localities, no study of molt for the species has been published previously.

MATERIALS

Detailed molt data were collected on live Scrub Jays and Blue Jays at Archbold Biological Station, Highlands County, Florida (lat. 27°10′), where both species are common permanent residents (Woolfenden 1969). A population of Scrub Jays has been studied intensively there since 1969 (Woolfenden 1974, 1975), and all Scrub Jays examined for molt already were banded, and most were of known age, sex, and breeding status. In 1976 and 1977, 63 juveniles were examined one to five times for a total sample of 112 juvenile Scrub Jay observations. During these same two years, 94 Scrub Jays, ages one year or older, were examined one to eight times for a total sample of 180 observations.

Blue Jays have not been studied in detail at Archbold Biological Station, and most of the individuals captured had not been marked. All previously unbanded Blue Jays were banded upon capture. In 1976 and 1977, 73 juveniles were examined one to five times for a total sample of 139 juvenile observations, and 143 yearling or older individuals were examined one to six times for a total sample of 195 observations. In 1976, of the 105 Blue Jays we examined, only 12 had been banded previously. One of these 12 was a yearling, and 11 were older. In 1977, of the 54 we examined 25 had been banded previously; six of these were yearlings.

Remex and rectrix molt data taken by Woolfenden from 56 marked Scrub Jays captured 76 times during the years 1971 through 1975 are used in certain analyses. Of these 56 individuals, 21 were captured again during 1976 and 1977. In order to acquire data from the spring months prior to concentrated field work, we examined 34 Scrub Jay specimens collected between January and April near the Archbold Biological Station. Seven Blue Jays collected in November and December near Whitfield, Santa Rosa County, Florida, were examined to provide information from late fall when Blue Jays were difficult to catch at the station. These specimens are located in the University of South Florida and Carnegie Museum of Natural History collections, respectively. The breeding data on Scrub Jays that we use span the time of our molt work (Woolfenden 1974, unpubl. field notes). The few data on breeding by Blue Jays obtained at the station in 1976 also are used.

METHODS

Florida Scrub Jays often breed in family groups in which non-breeding young from previous years help to rear later broods (Woolfenden 1974, 1975). When analyzing molt data, we separated Scrub Jays into seven classes: juveniles, male breeders, female breeders, older male helpers, older female helpers, yearling male helpers, and yearling female helpers. All breeders and all older helpers examined were at least two years old.

Pitelka (1946) described methods for distinguishing yearlings from older Blue Jays by plumage. The upper greater secondary coverts are unbarred in the juvenal plumage, but barred in the definitive plumage. Young Blue Jays that retain these coverts during the first prebasic molt can be recognized as yearlings. However, we found that most Blue Jays in Florida molt all the upper greater secondary coverts during the first prebasic molt. This made use of these coverts alone unreliable for ageing Florida birds. The alulae and upper greater primary coverts of the juvenal plumage also are unbarred and grayer on the tip than in the definitive plumage, and these feathers are not changed during the first prebasic molt of Florida Blue Jays. However, after nine months of wear, we found that we were unable to use these features for ageing in the field.

With existing information, only the sex of female Blue Jays can be determined from external characteristics, and then only when the females have a brood patch. Therefore, for this study we distinguish only three classes of Blue Jays, juveniles, breeding females, and yearling and older unsexed birds of unknown breeding status. The six known yearlings and 19 known older individuals captured in 1977 permitted comparison of the onset of molt between these age classes.

We follow the terminology of Humphrey and Parkes (1959) when describing the molts and plumages of Scrub Jays and Blue Jays. The sequence of events is as follows. Feather replacement starts when individuals are about 2.5 months old. This molt, the first prebasic [= post-juvenal of Dwight, in Humphrey and Parkes, 1959] is incomplete. About a year later, and then annually thereafter, these jays undergo a complete molt, the definitive prebasic [= post-nuptial of Dwight] molt. The primaries are numbered one through ten from proximal to distal; the secondaries are numbered one through ten from distal to proximal (Van Tyne and Berger 1975).

A numerical system similar to that of Ashmole (1962) and Newton (1966) was used to score each remex and rectrix from 0 to 5 (e.g., 0 = not dropped, 5 = completely regrown). A remex score was obtained for each bird by summing the individual scores for all 20 primaries and for both the left and right sixth secondary. Ligon and White (1974) used a similar system based on all 20 primaries and both the fifth and sixth secondaries. For Scrub Jays and Blue Jays, excluding the fifth secondaries results in scores more linearly related to date, which is important if recapture data and regression analysis are used to estimate the duration of molt. A remex score of zero indicates that remigial molt has not started, and an overall score of 110 indicates remigial molt is completed. Based on the remex score, each bird was assigned to a remex stage of 1 through 11, or 11+ (1 = remex score 1–10; 2 = remex score 11–20; . . . 11 = remex score 101–109; 11+ = remex score 110, all remiges new). In our analyses molt of other feathers is compared with remex stage.

Molt for the six body tracts was scored from 0 to 3 (0 = no molt, 1 = 1 to 3 feathers growing, 2 = every fourth feather growing, 3 = most of the tract with feathers growing) following Ainley et al. (1976). For the first prebasic molt separate scores were kept for several regions of three body tracts:

Spinal: pelvic, dorsal, interscapular, and cervical;
Capital: forehead, crown, nape, lores, auricular, and malar;
Ventral: submalar, cervical, sternal, and abdominal.

Using these numbers, a body intensity score was calculated for each bird by summing the scores for the six body tracts. Maximum scores of 51 for the first prebasic molt and 18 for the definitive prebasic molt are possible. The difference between maximum scores reflects the different number of regions scored. Mean body intensity score was compared to remex stage for the definitive molt to show when the greatest intensity of body molt occurred. For the first prebasic molt the body intensity score was compared to date and age from hatching to determine the timing and intensity of the replacement of juvenal plumage.

Molt of the alulae and the wing and tail coverts was scored only as present or absent. For both the first and definitive prebasic molts data were recorded for the alulae, upper greater primary coverts, upper greater secondary coverts, upper middle secondary coverts, lower primary coverts, lower secondary coverts, marginal coverts, and upper and lower tail coverts. For the first prebasic molt only, the upper middle primary coverts were scored also, and the lower greater and lesser primary coverts were scored separately.

During the definitive prebasic molt, all but a few body feathers are replaced within the time required to replace the remiges. Therefore, estimating the duration of remex molt gives an accurate estimate of the time required to replace virtually all feathers. Duration of the definitive prebasic molt was estimated on the basis of rate of remex molt in individual jays captured more than once, and by subjecting remex scores for all jays in active remigial molt to linear regression analysis.

The duration of remex molt was estimated indirectly using molting jays captured two or more times at least 5 days apart. The difference in remex scores between captures divided by the number of days between captures is the rate of molt and is given as points per day.

The timing of molt of each feather group is shown by tabulating the data as the percentage of birds molting those feathers during the first half (early) and last half (late) of each month. The timing of molt relative to the breeding season is shown by plotting the percentage of birds molting primaries, secondaries, rectrices, and body feathers against date on the same graph as a histogram of the number of active nests per week. The progression of the first prebasic molt is shown by plotting the mean body molt scores for half-month periods. The progression of the definitive prebasic molt is shown by plotting remex scores against date.

SCRUB JAY MOLTS

First Prebasic Molt

The first prebasic molt of Florida Scrub Jays is a partial molt that includes all body feathers, most of the alar and caudal tract coverts, a variable number of secondaries 8 through 10, and a variable number of rectrices (Table 1). No juvenile Scrub Jays were examined that molted primaries or upper greater primary coverts, and only three replaced either the lower greater primary coverts or alula feathers. New feathers in these regions were considered replacements for feathers lost accidentally.

The onset of the first prebasic molt was marked by loss of some marginal coverts and was followed quickly by molt of some feathers in the interscapular region of the spinal tract and the sternal region of the ventral tract. The timing and pattern of this molt in Florida Scrub Jays are shown in Table 1. The single individual examined in the first half of June had just started to molt in the spinal and ventral tracts, and in the marginal coverts. Of seven juveniles examined in the second half of June, one had not started to molt, five had just started molt in several body tracts, and one had feathers growing in all six body tracts. During late June, 12 additional Scrub Jays, though not handled, were scrutinized from a few centimeters distance, and two appeared not to have started molt. The others were molting in at least a few body tracts. Although there was some variation, most Florida Scrub Jays began the first prebasic molt in June. Scrub Jays fledging in late May or June probably began molt in July as shown by an individual examined on 20 July that had not started molt. Unfortunately the exact age of this individual was not known. All 16 individuals examined in August were molting. Scrub Jays finished replacing the upper wing coverts during late August and early September. All 55 juveniles examined after 15 August had replaced all the upper secondary coverts. By early September some individuals had dropped all

TABLE 1

PERCENTAGE OF JUVENILE FLORIDA SCRUB JAYS EXAMINED IN SUCCESSIVE HALF-MONTHS MOLTING FEATHERS IN VARIOUS REGIONS DURING THE FIRST PREBASIC MOLT

	June		July		Aug.		Sept.		Oct.		Nov.	
No. jays	1 (1)	2 (7)	1 (25)	2 (19)	1 (6)	2 (10)	1 (27)	2 (6)	1 (1)	2 (10)	1 (0)	2 (3)
Primaries	0	0	0	0	0	0	0	0	0	0	—[1]	0
Secondaries	0	0	0	0	17	90	59	33	100	0	—	0
Rectrices	0	0	4	37	67	50	44	50	100	0	—	0
Upper greater primary coverts	0	0	0	0	0	0	0	0	0	0	—	0
Upper middle primary coverts	0	0	36	42	33	0	0	0	0	0	—	0
Upper greater secondary coverts	0	0	40	42	67	20	11	0	0	0	—	0
Upper middle secondary coverts	0	14	44	68	50	0	4	0	0	0	—	0
Lower greater primary coverts	0	0	8	0	0	0	0	0	0	0	—	0
Lower lesser primary coverts	0	0	56	26	33	20	11	17	0	0	—	0
Lower secondary coverts	0	14	24	37	50	30	19	0	0	0	—	0
Marginal coverts	100	57	88	84	83	90	33	0	0	0	—	0
Alulae	0	0	0	0	0	10	0	0	0	0	—	0
Upper tail coverts	0	0	28	47	33	70	74	83	0	20	—	0
Lower tail coverts	0	0	36	58	83	90	89	67	100	0	—	0
Capital: forehead	0	14	32	63	67	50	56	33	100	0	—	0
crown	0	0	32	58	83	90	63	50	100	0	—	33
nape	0	14	16	58	67	90	85	83	100	0	—	0
lores	0	29	44	68	67	40	7	0	0	0	—	0
auricular	0	14	0	26	67	90	93	67	100	10	—	0
Humeral	0	43	72	74	100	100	89	83	100	0	—	0
Femoral	0	14	44	68	83	100	100	100	100	20	—	100
Crural	0	14	68	79	100	70	48	0	100	0	—	0
Spinal: pelvic	0	14	56	63	83	100	93	83	100	50	—	33
dorsal	0	43	60	68	100	100	96	100	100	70	—	67
interscapular	100	57	72	84	100	100	89	100	100	40	—	0
cervical	0	0	24	53	100	100	100	67	100	0	—	0
Ventral: submalar	0	0	28	63	100	90	100	50	100	10	—	0
cervical	0	43	80	89	100	100	100	100	100	10	—	0
sternal	100	43	84	89	100	100	100	100	100	60	—	67
abdominal	0	29	24	58	67	100	100	100	100	20	—	0

[1] Dash = no data available.

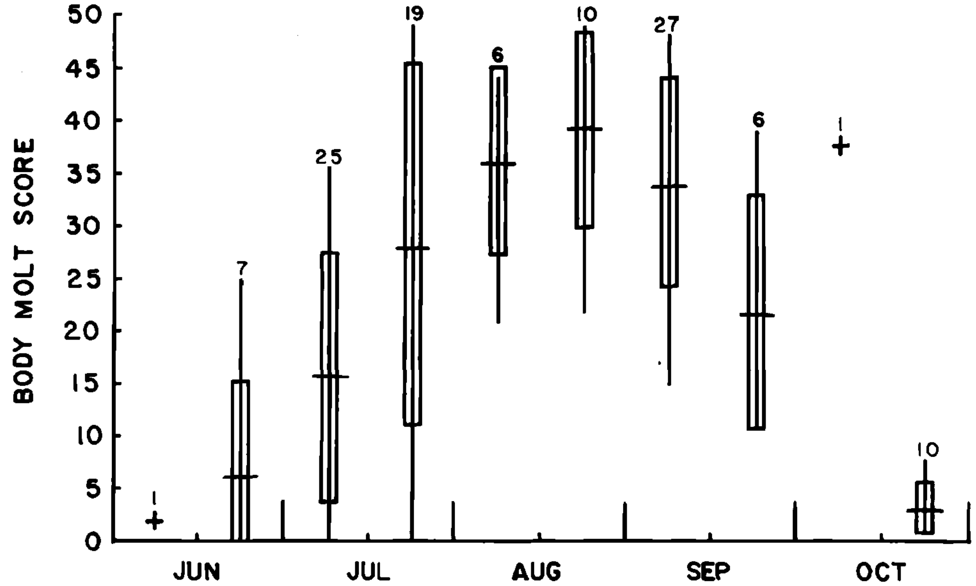

Fig. 1. Intensity of the first prebasic body molt in juvenile Florida Scrub Jays examined in successive half-months. Intensity is described by the mean body score (horizontal line), range (vertical line), and one standard deviation on either side of the mean (rectangle). Numbers above ranges are sample sizes.

juvenal body plumage, and some had completed growth of new feathers on the capital, humeral, and crural tracts. Others still had juvenal feathers in the capital tract in late September. All 10 jays examined in late October had some feathers growing, but different individuals had completed growth in different feather regions. Five of the 10 late October jays had only a few feathers still growing. The three jays examined in late November still were growing a few feathers in some body tracts. Thus, growth of the last few feathers seems to be drawn out over a month or more.

The mean body molt intensity score peaked in August and decreased through October (Fig. 1). The single value for the first half of October was for a jay from a late brood. This jay was in an earlier stage of molt than most jays at that time.

Molt of the proximal secondaries occurred during August, September, and October. Some Scrub Jays completed growth of molted secondaries by early September. Of 42 juveniles examined after 1 September, 41 had molted secondaries 9 and 10, 11 also had molted secondary 8, and one had molted only secondary 10. With the one exception excluded, secondary 9 was molted before 10, and secondary 8 was molted either before 9 or after 10. Secondaries 1–7 are not replaced.

Normal rectrix molt was first recorded in early July when two of 25 Scrub Jays examined had dropped the central pair of rectrices. Of 48 jays with seemingly normal tail molt examined after 15 August, seven also had molted the pair of rectrices immediately lateral to the central two. One jay captured in early September had molted no tail feathers. However, this was an individual from a late brood, and by late October it had replaced the central pair. Thus, all 43 juveniles examined after 1 September had replaced at least the central pair of rectrices. Some juveniles completed growth of molted rectrices by early September. The outer four pairs of rectrices were not included in the first prebasic molt, although six jays had replaced some or all of these feathers after their accidental loss.

As most of the juveniles examined were banded as nestlings, it was possible to compare the timing of molt of each feather group to age from hatching (Table 2). Molt apparently begins no earlier than two months after hatching. The two individuals caught when 61 to 75 days old had just started marginal covert molt, and one had started molt in the interscapular region of the spinal tract. Of 10 individuals captured in the 76 to 90 day age bracket, two had not started molt, three had started molt in some body tracts, and one had started molt in all six body tracts. All 19 jays examined when 91 to 105 days old had started molt. Thus, most Scrub Jays started the first prebasic molt between 60 and 90 days after hatching. The intensity of body molt increased to a peak from 121 to 135 days after hatching and then decreased (Fig. 2). The most intense replacement of juvenal plumage occurred in a 75-day period between 90 and 166 days after hatching. Molt of the proximal secondaries occurred between 105 and 166 days of age. The last juvenal body feathers to be molted were in the auricular region of the capital tract and were dropped between 120 and 151 days after hatching. Some individuals completed growth of new feathers in the capital, humeral, and crural tracts when between 135 and 166 days old. Although nine jays between 180 and 211 days of age still had some feathers growing, all had completed growth of the first basic plumage in some feather regions. All four jays captured when 196 to 210 days old had a few feathers still growing, as did both jays captured when 226 to 240 days old. Thus, it appears that the first prebasic molt requires from 140 to 170 days from start to completion.

The central tail feathers were lost as early as 91 days post-hatching and were fully grown as early as 136 days post-hatching. Some young jays were growing the central pair when 151 to 165 days old. The few individuals that replaced the second pair dropped them between 120 and 166 days of age.

DEFINITIVE PREBASIC MOLT

PRIMARIES AND SECONDARIES

Remigial molt, which is highly symmetrical, started with the loss of primary 1 in Scrub Jays. The primaries were molted in sequence, with from one to three growing simultaneously in each wing. Individuals began remigial molt between late April and late June and continued into August or September (Table 3). Secondary molt usually started about the time primary 4 was dropped. As many as four secondaries per wing grew simultaneously. Generally, secondary 8 was the first secondary to be dropped, but occasionally secondary 1 was dropped first. Secondary 9 was dropped soon after 8, and sometimes before 1. After 9, secondaries 7, 2, and 10 were dropped quickly in that order. Following 10, secondaries 3 through 6 were dropped in order. Secondary 6 was the last remex to be replaced.

The mean number of primaries growing per wing increased quickly to 3.1 at remex stage 3, decreased slightly when the secondaries started molting, and returned to 2.8 by stage 9, after which it decreased rapidly (Table 3). The mean

TABLE 2

Percentage of Juvenile Florida Scrub Jays of Different Ages Molting Feathers in Various Regions During the First Prebasic Molt

	Days from hatching											
No. jays	61–75 (2)	76–90 (10)	91–105 (19)	106–120 (14)	121–135 (16)	136–150 (20)	151–165 (10)	166–180 (2)	181–195 (5)	196–210 (4)	211–225 (0)	226–240 (2)
Primaries	0	0	0	0	0	0	0	0	0	0	—[1]	0
Secondaries	0	0	0	7	75	60	40	0	0	0	—	0
Rectrices	0	0	11	57	88	40	10	50	0	0	—	0
Upper greater primary coverts	0	0	0	0	0	0	0	0	0	0	—	0
Upper middle primary coverts	0	0	47	64	0	0	0	0	0	0	—	0
Upper greater secondary coverts	0	10	58	57	31	5	0	0	0	0	—	0
Upper middle secondary coverts	0	20	53	86	13	0	0	0	0	0	—	0
Lower greater primary coverts	0	0	11	0	0	0	0	0	0	0	—	0
Lower lesser primary coverts	50	40	58	14	13	15	20	0	0	0	—	0
Lower secondary coverts	0	10	37	36	19	30	10	0	0	0	—	0
Marginal coverts	100	60	89	93	63	45	10	0	0	0	—	0
Alulae	0	0	0	0	6	0	0	0	0	0	—	0
Upper tail coverts	0	10	26	71	69	80	50	50	20	0	—	0
Lower tail coverts	0	20	32	93	100	90	70	0	0	0	—	0
Capital: forehead	0	20	42	100	75	40	40	0	0	0	—	0
crown	0	0	42	86	94	70	40	0	0	25	—	0
nape	0	10	21	86	100	90	70	0	0	0	—	0
lores	0	30	53	93	38	10	0	0	0	0	—	0
auricular	0	10	0	43	100	90	80	0	20	0	—	0
Humeral	0	40	89	79	100	95	70	50	0	0	—	0
Femoral	0	10	63	93	100	100	100	50	0	50	—	100
Crural	0	30	89	100	75	50	20	0	0	0	—	0
Spinal: pelvic	0	30	58	93	94	100	80	50	40	75	—	0
dorsal	0	40	74	93	94	100	100	100	60	50	—	100
interscapular	50	50	89	100	100	95	80	100	0	50	—	0
cervical	0	10	32	86	100	100	90	0	0	0	—	0
Ventral: submalar	0	0	42	100	100	95	80	0	20	0	—	0
cervical	0	50	100	100	100	100	100	50	20	0	—	0
sternal	0	80	89	100	100	100	100	100	80	25	—	50
abdominal	0	30	26	86	94	100	100	50	20	0	—	0

[1] Dash = no data available.

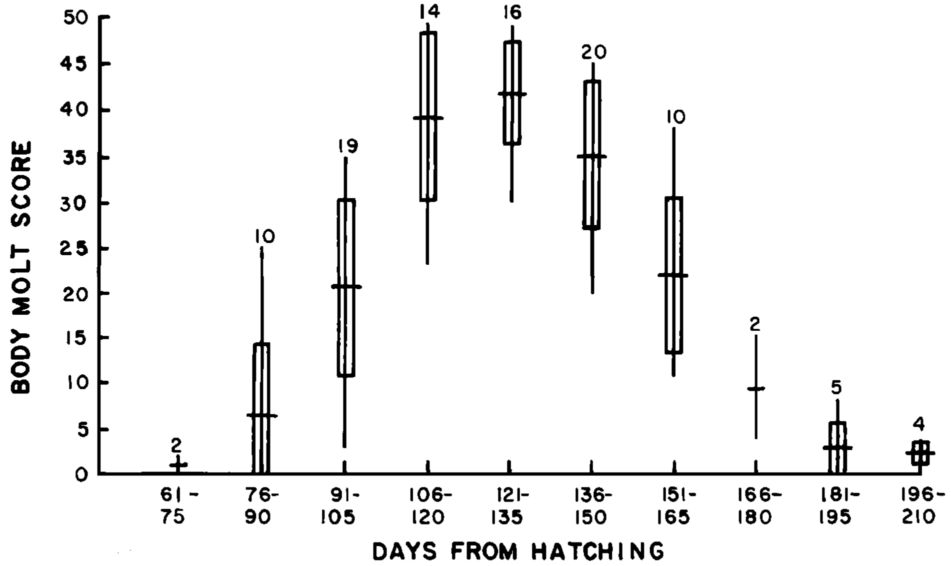

Fig. 2. Intensity of the first prebasic molt in juvenile Florida Scrub Jays of different ages. Intensity is described by the mean body score (horizontal line), range (vertical line), and one standard deviation on either side of the mean (rectangle). Numbers above ranges are sample sizes.

number of secondaries growing per wing increased to a peak of 3.6 by remex stage 7 and then decreased.

RECTRICES

Molt of the rectrices began between remex stages 3 and 5 (Table 4). Two of eight birds examined with primary 4 but not primary 5 growing had molted at least the central pair of rectrices, and seven of eight birds examined with primary 5 but not 6 growing had begun tail molt. Tail molt was centrifugal, and finished with pair 6 about the same time as the remiges finished growing. Frequently, tail feathers were lost accidentally. We considered all tail molt recorded during remex stages 1, 2, and 11+, and molt of the outer rectrices in remex stages 3–5 to be adventitious.

As many as 10 rectrices may grow simultaneously. The mean number increased to 7.4 by remex stage 7 and then decreased after remex stage 9 (Table 4). The peak number of growing rectrices coincided with the maximum mean number of growing remiges (6.1 per wing).

BODY FEATHERS, ALULAE, AND COVERTS

Table 5 gives the percentage of adult Scrub Jays in each remex stage that had feathers growing in each of the areas examined. The upper greater primary coverts were molted with their corresponding primaries. Individuals began molting upper secondary and marginal coverts about the same time that the first secondaries were dropped, but upper covert molt finished first. No individuals had any body molt before primary 3 dropped. Four of eight birds handled when primary 4 was growing had begun body molt, and all eight individuals handled when

TABLE 3

PERCENTAGE OF ADULT FLORIDA SCRUB JAYS IN EACH REMEX STAGE OF THE DEFINITIVE PREBASIC MOLT REPLACING PRIMARIES AND SECONDARIES

		Remex stage[1]											
	No. jays	1 (42)	2 (20)	3 (14)	4 (17)	5 (16)	6 (19)	7 (16)	8 (17)	9 (12)	10 (10)	11 (15)	11+ (17)
Primary	1	100	90	64	0	0	0	0	0	0	0	0	0
	2	62	100	86	0	0	0	0	0	0	0	0	0
	3	2	70	100	59	0	0	0	0	0	0	0	0
	4	0	0	57	100	63	0	0	0	0	0	0	0
	5	0	0	0	35	100	58	0	0	0	0	0	0
	6	0	0	0	0	69	100	88	6	8	0	0	0
	7	0	0	0	0	0	42	100	76	8	0	0	0
	8	0	0	0	0	0	0	63	100	92	30	0	0
	9	0	0	0	0	0	0	0	47	100	90	13	0
	10	0	0	0	0	0	0	0	6	67	90	13	0
Secondary	1	0	0	0	29	100	68	19	6	0	0	0	0
	2	0	0	0	0	31	74	88	65	8	0	0	0
	3	0	0	0	0	0	0	56	76	83	10	0	0
	4	0	0	0	0	0	0	13	35	100	70	0	0
	5	0	0	0	0	0	0	0	0	0	90	90	0
	6	0	0	0	0	0	0	0	0	0	50	100	0
	7	0	0	0	0	13	26	88	59	33	0	0	0
	8	0	5	21	71	81	47	6	6	0	0	0	0
	9	0	0	7	41	81	74	25	0	17	0	0	0
	10	0	0	0	0	0	5	69	71	58	0	0	0
Mean no. growing													
Primaries		1.6	2.6	3.1	1.9	2.3	2.0	2.5	2.4	2.8	2.1	0.3	0.0
Secondaries		0.0	0.0	0.3	1.4	3.1	2.9	3.6	3.2	3.0	2.2	1.5	0.0

[1] Remex stages based on groupings of remex scores (i.e., 1 = Remex Scores 1–10, 2 = Remex Scores 11–20, . . . , 11 = Remex Scores 101–109, 11+ = Remex Score 110).

TABLE 4

PERCENTAGE OF ADULT FLORIDA SCRUB JAYS IN EACH REMEX STAGE OF THE DEFINITIVE PREBASIC MOLT REPLACING RECTRICES

		Remex stage[1]											
	No. jays	1 (33)	2 (17)	3 (10)	4 (14)	5 (16)	6 (19)	7 (14)	8 (16)	9 (11)	10 (8)	11 (15)	11+ (17)
Rectrix													
Left	6	3	0	0	0	6	5	21	44	100	100	67	0
	5	0	0	10	7	0	5	50	75	100	100	20	0
	4	0	0	0	0	0	21	86	75	100	38	0	6
	3	3	0	0	7	19	95	79	81	64	13	0	0
	2	0	0	0	14	75	95	93	50	0	0	0	0
	1	3	0	10	50	100	89	36	0	0	0	0	0
Right	1	9	0	30	57	88	89	21	0	0	0	0	0
	2	0	6	0	14	88	95	100	50	18	0	0	0
	3	0	0	10	7	13	84	93	75	64	13	0	0
	4	0	0	0	7	6	37	86	81	82	38	7	0
	5	3	6	10	0	0	11	50	75	91	100	20	0
	6	3	12	10	0	0	0	29	38	91	100	73	6
Mean no. growing		0.2	0.2	0.8	1.6	3.9	6.3	7.4	6.4	7.1	5.0	1.9	0.1

[1] Determined as described in footnote, Table 3.

TABLE 5

PERCENTAGE OF ADULT FLORIDA SCRUB JAYS IN EACH REMEX STAGE OF THE DEFINITIVE PREBASIC MOLT REPLACING BODY FEATHERS, ALULAE, AND COVERTS

	Remex stage[1]											
No. jays	1 (14)	2 (6)	3 (2)	4 (11)	5 (13)	6 (17)	7 (13)	8 (13)	9 (10)	10 (8)	11 (15)	11+ (17)
Upper greater primary coverts	50	100	100	100	100	100	100	92	40	13	0	0
Upper greater secondary coverts	0	17	0	82	92	53	46	15	0	0	0	0
Upper middle secondary coverts	0	0	0	0	62	82	62	31	10	0	0	0
Lower primary coverts	0	0	0	36	77	76	92	92	90	88	20	0
Lower secondary coverts	0	0	0	9	69	76	100	100	90	13	20	6
Marginal coverts	0	0	0	64	100	88	92	85	90	13	0	0
Alulae	0	0	0	0	0	6	77	85	80	38	0	0
Capital tract	0	0	0	0	8	71	92	100	100	100	93	24
Humeral tract	0	0	0	45	100	94	100	100	100	100	93	29
Femoral tract	0	0	0	36	85	94	92	100	100	100	100	47
Crural tract	0	0	0	45	100	94	100	92	80	50	7	6
Spinal tract	0	17	0	27	100	94	100	100	100	100	100	35
Ventral tract	0	0	0	18	92	100	100	100	100	100	100	35
Upper tail coverts	0	0	0	9	77	88	100	100	100	63	13	0
Lower tail coverts	0	0	0	18	54	82	92	100	100	100	67	12

[1] Determined as described in footnote, Table 3.

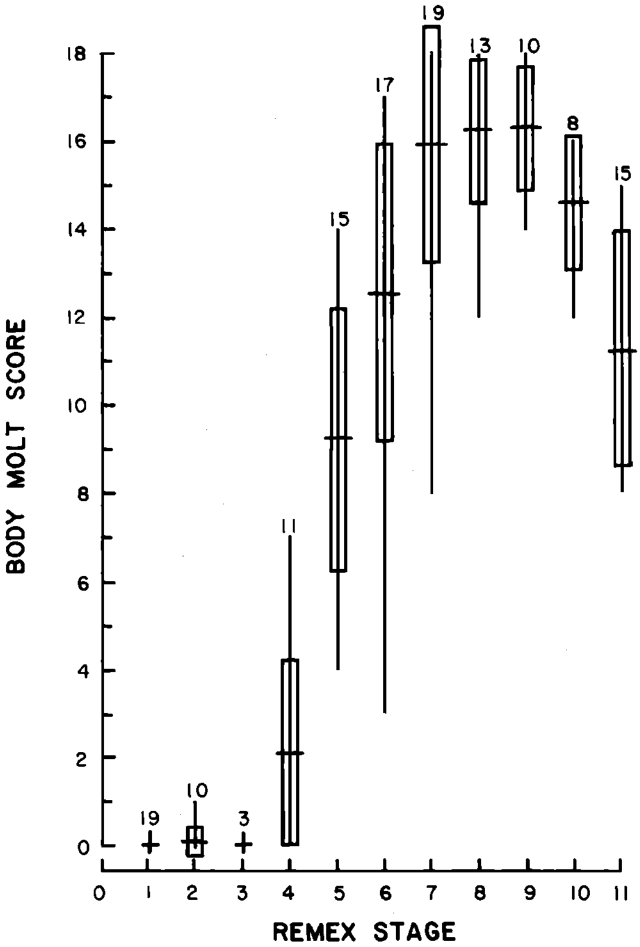

Fig. 3. Intensity of body molt in adult Florida Scrub Jays during different remex stages of the definitive prebasic molt. Intensity is described by the mean body score (horizontal line), range (vertical line), and one standard deviation on either side of the mean (rectangle). Numbers above ranges are sample sizes.

primary 5 was growing had begun body molt. Molt in the capital tract and alulae started between the loss of primaries 6 and 9. Regrowth of the body tracts extended beyond completion of remex growth. Tail covert molt began soon after the onset of tail molt during remex stage 4. The intensity of body molt increased from remex stage 4 to a peak at stages 8 and 9 and decreased through stage 11 (Fig. 3). Body molt reached maximum intensity during the same three remex stages in which the maximum number of remiges and rectrices were growing (Fig. 3, Table 5).

Duration of Molt

We plotted remex score against date for individual Scrub Jays from five classes, based on birds caught more than once, and then connected remex scores for the

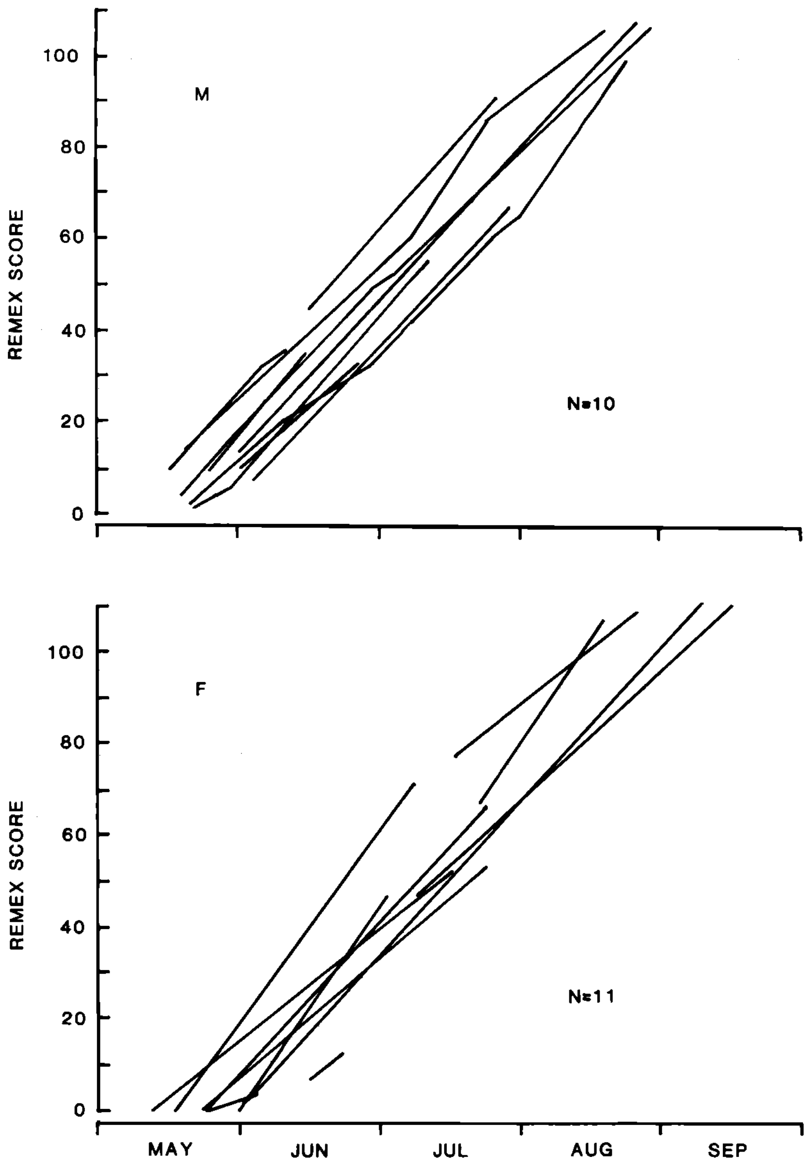

Fig. 4. Remex scores of individual Florida Scrub Jay breeders examined two or more times during one definitive prebasic molt (M = male breeders; F = female breeders).

same individual on successive capture dates (Figs. 4, 5). Changes in the slope of a line reflect changes in rate of remex molt. Unfortunately, no older female helpers were caught more than once in the same molt cycle.

A mean rate of molt in points per day was determined for each of the five classes of Scrub Jays (Table 6). Only rates calculated from jays captured in active molt were used, and only one rate was calculated for each individual based on

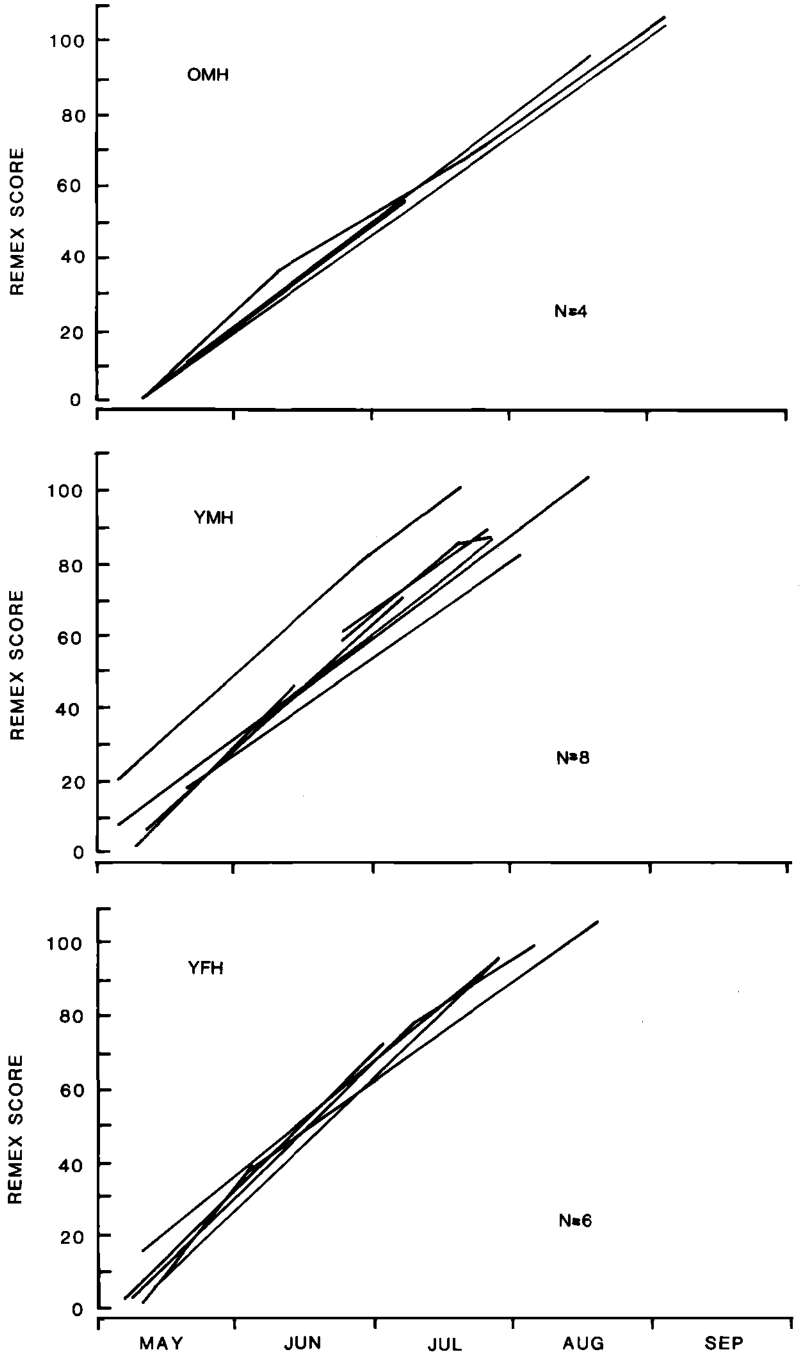

Fig. 5. Remex scores of individual Florida Scrub Jay helpers examined two or more times during one definitive prebasic molt (OMH, older male helpers; YMH, yearling male helpers; YFH, yearling female helpers).

TABLE 6

MEAN RATE OF THE DEFINITIVE PREBASIC MOLT IN FLORIDA SCRUB JAYS, BASED ON RECAPTURE DATA AND REGRESSION ANALYSIS

	Recapture			Regression		
Class	n	rate[1]	s.d.	n	rate	s.d.
Male breeders	10	1.064	0.086	49	0.99	0.00021
Female breeders	4	1.020	0.284	25	1.104	0.00074
Older male helpers	2	0.893	0.089	11	0.852	0.00033
Yearling male helpers	8	0.996	0.138	25	0.918	0.00036
Yearling female helpers	6	1.054	0.137	21	1.040	0.00038
Combined	30	1.03	0.145			

[1] Change in remex score per day.

the change in remex score between first and last capture. A comparison of these rates using a test for means with unequal variances (Sokal and Rohlf 1969:372), was not significant (F = 1.29; d.f. = 4, 5.76; $P > 0.05$). Thus, jays in all five classes apparently replace their primaries at the same rate. Therefore, a mean remex molt rate of 1.03 points per day (s.d. = 0.145, range = 0.71–1.44, n = 30) was calculated for all five classes combined. At this rate remex molt would be completed in 107 days. If a Scrub Jay were to maintain either of the extreme rates, remex molt would be completed in 76 or 155 days. A late-breeding female with nestlings exhibited the slowest rate, 0.71 points per day. However, this calculation is based on observations made only 7 days apart. Two breeding males had slow rates during the early part of remex molt but increased their rates later. One male changed only 18 points in 23 days (0.78 p/d) and 13 points in the next 16 days (0.81 p/d). The other male changed only 8 points in 12 days (0.67 p/d). These slow rates for all three birds occurred while they were tending active nests. The two males increased their rates to 67 points in 58 days (1.16 p/d) and 47 points in 40 days (1.18 p/d) following nesting. The increase in rate following nesting suggests that breeding males may protract molt if molt and breeding overlap and then increase the rate of molt after breeding is finished. Breeding females that protracted molt while nesting probably also increased their molt rate following nesting. An older male helper Scrub Jay also had a slow rate of 0.74 points per day (32 p/43 days), but his rate increased to 41 points in the next 45 days (0.91 p/d). This older male helper averaged 0.84 points per day over the 88 days between first and last capture.

Remex molt was most rapid for a breeding female who fledged young on the late date of 2 June. She had not started molt on 30 May, yet had a remex score of 45 by 1 July, indicating a remex molt rate of at least 1.44 points per day. Another breeding female changed 39 points in 28 days (1.39 p/d) between 21 July and 18 August, following successful breeding. Three individuals, a breeding male, a yearling male helper, and a yearling female helper, that were captured more than 30 days apart had increased their remex scores between 1.24 and 1.27 points per day. If these fast rates were maintained through remex molt, the process would be completed in less than 90 days. A yearling female helper increased her remex score 35 points in 24 days (1.45 p/d) during the early part of her remex molt, but

TABLE 7

VARIATION IN THE RATE OF MOLT FOR 10 INDIVIDUAL FLORIDA SCRUB JAYS

Class	Rate[1] between successive captures			
Male breeder	1.00 (12)[2]	1.14 (29)	1.00 (59)	
Male breeder	1.06 (49)	1.33 (15)	0.81 (27)	
Male breeder	0.78 (23)	0.81 (16)	1.08 (26)	1.11 (32)
Male breeder	0.67 (12)	1.18 (40)		
Older male helper	0.74 (43)	1.00 (5)	0.90 (40)	
Yearling male helper	0.93 (56)	1.04 (26)		
Yearling male helper	1.12 (56)	0.90 (20)		
Yearling female helper	0.94 (48)	1.03 (32)		
Yearling female helper	1.46 (24)	1.02 (57)		
Yearling female helper	1.26 (35)	1.27 (23)		

[1] Points per day.

[2] Number in parentheses = days between successive captures.

then slowed to 58 points in the next 57 days (1.02 p/d). Overall her average rate was 1.15 points per day, which indicates remex molt would take about 96 days.

Remex molt rates based on Scrub Jays captured both early and late in their molt cycles are nearly identical to those calculated from the total sample. Nine birds that were caught from two to six times, whose remex scores had increased more than 80 points, averaged 1.06 points per day (s.d. = 0.06, range = 0.96–1.15 p/d). The sample included four breeding males, one breeding female, one older male helper, one yearling male helper, and two yearling female helpers.

Fluctuations in the rate of molt were examined for 10 Scrub Jays captured three or more times (Table 7). Two breeding males showed the greatest fluctuations, their fastest rates being 1.8 and 1.4 times their slowest. The rates were slow during nesting and increased afterward. The fastest rate for an individual was 2.2 times the slowest rate of a different individual. Several Scrub Jays maintained relatively constant rates of molt between captures.

Remex scores for all birds captured in active molt were plotted against date, and the plots subjected to linear regression analysis (Table 6). Analysis of covariance shows that the rates of molt for the five classes did not differ statistically ($F = 1.485$; d.f. = 4, 122; $P > 0.05$, Snedecor and Cochran 1967). A mean rate based on the total sample was not calculated because of the spread in the start of molt within the population. The onset of molt must by synchronized in order for regression analysis to estimate the duration of molt accurately, or the duration is overestimated (Newton 1966; Pimm 1976). The rates of molt based on the regression analysis are similar to those calculated from recapture data.

Based on these calculations, most Scrub Jays probably complete remigial molt in 95 to 115 days. The rapid molt exhibited by a few Scrub Jays suggests that some individuals may replace their remiges in less than 90 days; the slow rate of an older male helper suggests that a few jays may take more than 130 days.

CHRONOLOGY OF MOLT

Some Scrub Jays began molting in late April, and all birds were molting by the last half of June (Table 8). None of 34 Scrub Jays collected in central Florida between 1 January and 30 April was molting. The earliest record of normal molt

TABLE 8

PERCENTAGE OF ADULT FLORIDA SCRUB JAYS EXAMINED IN SUCCESSIVE HALF-MONTHS MOLTING FEATHERS IN VARIOUS REGIONS DURING THE DEFINITIVE PREBASIC MOLT

	May		June		July		Aug.		Sept.		Oct.		Nov.	
No. jays	1 (25)	2 (7)[1]	1 (20)	2 (16)	1 (22)	2 (29)	1 (3)	2 (11)	1 (7)	2 (4)	1 (0)	2 (8)	1 (0)	2 (3)
Primaries	44	83	97	100	100	100	67	27	0	25	—[2]	0	—	0
Secondaries	0	0	41	94	100	100	100	91	57	50	—	0	—	0
Rectrices	0	8	41	94	100	100	100	73	71	50	—	0	—	0
Upper greater primary coverts	—	57	83	100	100	62	33	0	0	0	—	0	—	0
Upper greater secondary coverts	—	14	38	56	50	24	0	0	0	0	—	0	—	0
Upper middle secondary coverts	—	0	7	63	59	34	0	0	0	0	—	0	—	0
Lower primary coverts	—	0	24	69	82	100	67	27	0	0	—	0	—	0
Lower secondary coverts	—	0	17	56	91	83	33	18	14	25	—	0	—	0
Marginal coverts	—	0	38	81	91	79	0	9	0	0	—	0	—	0
Alulae	—	0	0	6	36	79	33	0	0	0	—	0	—	0
Capital tract	0	0	3	31	73	100	100	100	71	75	—	0	—	0
Humeral tract	0	0	31	88	100	100	100	100	86	50	—	13	—	0
Femoral tract	0	0	24	75	95	100	100	100	100	100	—	13	—	33
Crural tract	0	0	34	75	86	100	33	9	14	0	—	0	—	0
Spinal tract	0	0	28	88	100	100	100	100	100	50	—	13	—	33
Ventral tract	0	0	17	88	100	100	100	100	100	100	—	13	—	0
Upper tail coverts	—	0	14	75	95	100	33	9	14	0	—	0	—	0
Lower tail coverts	—	0	17	56	86	100	100	73	29	75	—	0	—	0

[1] Sample size equals 12 for remiges and rectrices during the second half of May.

[2] Dash = no data available.

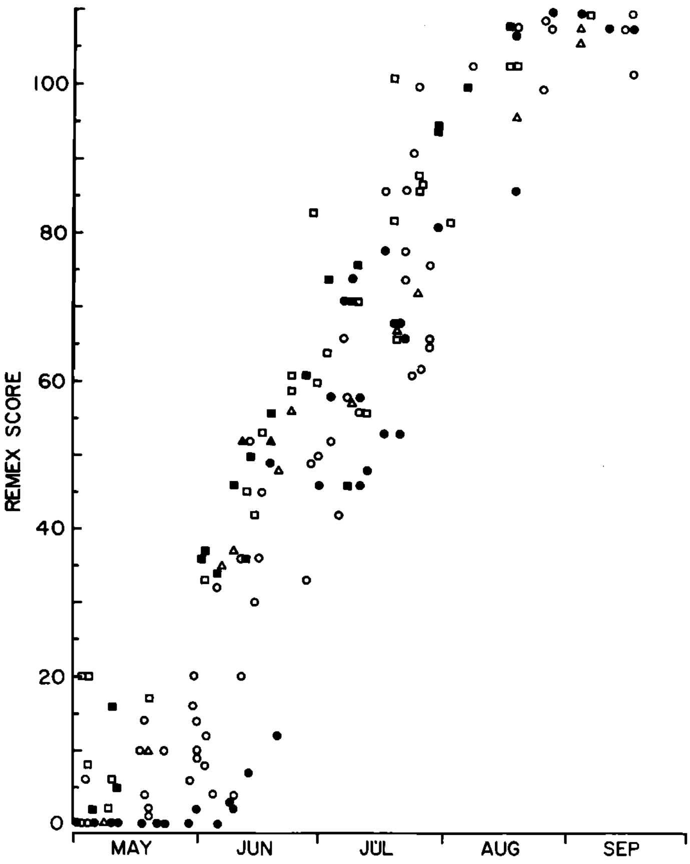

Fig. 6. Remex scores for adult Florida Scrub Jays examined during the definitive prebasic molt. Six classes are distinguished: male breeders (open circles), female breeders (closed circles), older male helpers (open triangles), older female helpers (closed triangles), yearling male helpers (open squares), yearling female helpers (closed squares). (Data for 1976 only.)

by a Florida Scrub Jay was of a yearling male helper captured on 4 May. He was growing the first three primaries (remex score 20), indicating molt had begun sometime in mid-April. Body molt was first noted on jays captured in the first half of June, and all individuals had some body molt in July and August. Some individuals were finishing remex molt as early as the end of August. By late August some Scrub Jays were replacing all body feathers, and some appeared to have all new body plumage. By late September all jays appeared to be in fresh plumage although they still were growing feathers at least in the ventral and femoral tracts.

The progression of molt in the population was illustrated by plotting remex scores against date (Fig. 6). In any half-month period from May to August several remex stages were represented by several individuals. The onset of molt was spread over a two-month period. The relationship between the onset of molt and age, sex, and breeding status was examined by dividing Scrub Jays into six classes

TABLE 9

PERCENTAGE OF ADULT FLORIDA SCRUB JAYS EXAMINED IN SUCCESSIVE HALF-MONTHS THAT HAD STARTED THE DEFINITIVE PREBASIC MOLT

	May				June			
	1		2		1		2	
Class	n	%	n	%	n	%	n	%
Male breeder	4	25	25	80	16	100	5	100
Female breeder	6	0	19	42	11	73	2	100
Older male helper	4	0	6	100	2	100	2	100
Older female helper	0	—	0	—	1	100	1	100
Yearling male helper	4	100	4	100	3	100	5	100
Yearling female helper	4	75	2	100	4	100	2	100

(Table 9). Yearling helpers, regardless of sex, began molting by mid-May. Yearlings, which are entering their first complete molt, tended to begin molting earlier than older individuals. The two older female helpers examined in June had remex scores in the low fifties suggesting they began molting in early May. Older male helpers and most male breeders began molting in May. One male breeder probably did not start molt until early June as he had a remex score of only 4 on 10 June. Female breeders began molting in late May to late June. The variation in the onset of molt between the classes described here is reflected in the distribution of scores for each class (Fig. 6). On a given date yearling Scrub Jays tend to have higher remex scores than older individuals, and breeding females tend to have the lowest scores. However, considerable overlap exists between classes, and a jay from any class may have the highest or lowest score on a given date. The synchronous onset of molt among helpers suggests that its timing is independent of the breeding stage of the pair being helped. The extended period during which breeders may begin molting suggests that the onset of their molt may be modified by breeding.

Overlap between molt and breeding was examined for the entire study population, including the non-breeding helpers, and for the early and late breeding males and females as groups and as individuals. In contrast to Scrub Jays many birds in Florida, including the Blue Jay, have active nests in July and August. For Florida Scrub Jays nesting begins in March, peaks in April, and ends in June (Woolfenden 1974). Renesting following failures, and the occasional true second brood attempts (Stallcup and Woolfenden 1978) are confined to these four months. For the population as a whole considerable overlap exists between breeding and molt, especially of primaries (Fig. 7). Even when the non-breeding helpers (Fig. 7: dashed-line area) are excluded overlap is extensive.

When information for breeders only is subdivided both by sex and by time of nesting (Table 10), important differences between the sexes are revealed. Breeding males began molting during mid-May regardless of their stage of nesting (2 × 2 contingency test, $\chi^2 = 0.07$, $P > 0.05$). Breeding females who finished nesting by mid-May began molting from mid-May to early June, but those who nested into June tended to delay the onset of molt (2 × 2 contingency test, $\chi^2 = 6.285$, $P < 0.05$).

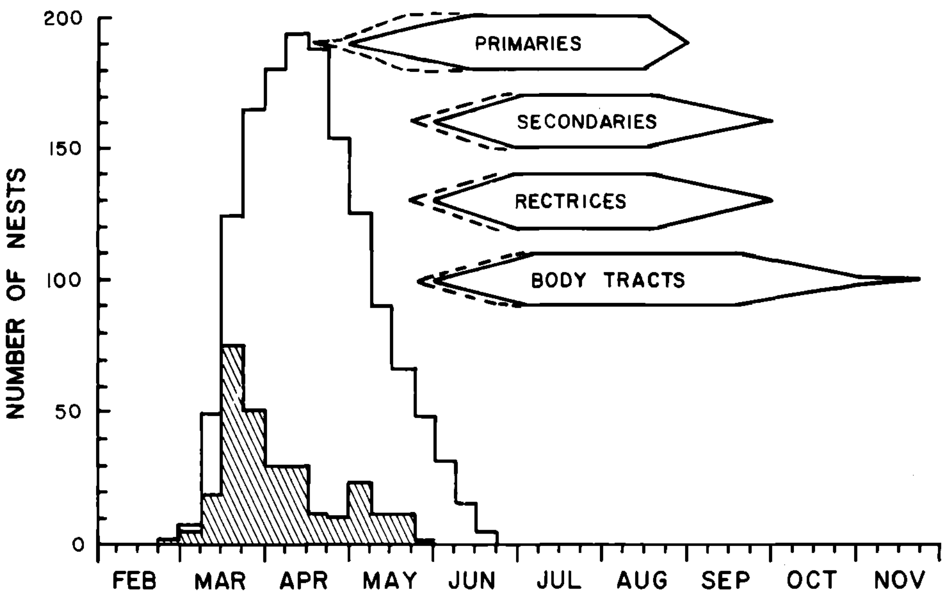

Fig. 7. The timing of breeding and the definitive prebasic molt in Florida Scrub Jays. Four regions of the plumage are distinguished. The width of the bar for each region indicates the proportion of birds molting those feathers. When a bar is at maximum width, all birds were molting those feathers. The areas enclosed by dashed lines are for the non-breeding helpers only. Number of active nests per week (open area), and week of completion of clutches (hatched area) are shown by the histogram.

We examined relationships between molt and nesting for breeders regardless of calendar time by plotting remex score relative to nesting (Fig. 8). We used only second or later nesting attempts, and in order to increase sample sizes, we used jays from 1973 as well as 1976. Clearly, even when nesting late in the breeding season, females do not progress as far into molt as their mates. A slope

TABLE 10

Percentage of Male and Female Florida Scrub Jay Breeders in Successive Half-months that Had Started the Definitive Prebasic Molt

	May				June			
	1		2		1		2	
Class	n	%	n	%	n	%	n	%
Male breeder before 15 May[1]	2	50	16	81	2	100	2	100
Male breeder after 1 June	2	0	8	100	8	100	3	100
Female breeder before 15 May	3	0	5	100	3	67	1	100
Female breeder after 1 June	2	0	8	12	6	83	1	100

[1] Time when nesting was completed.

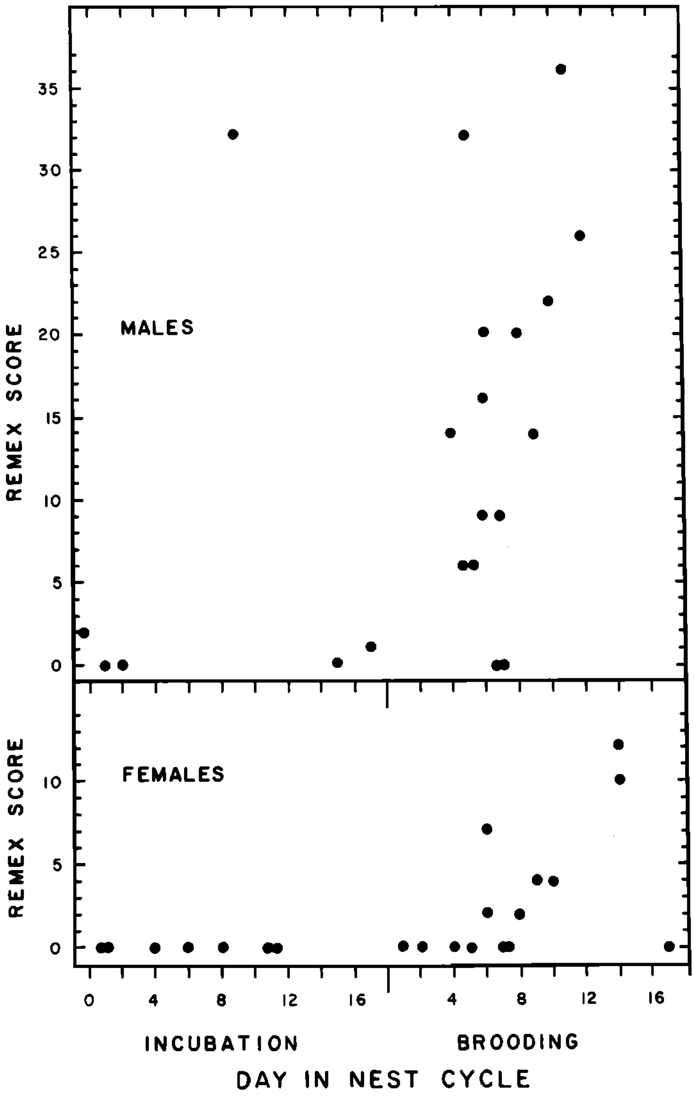

Fig. 8. Remex scores for late-nesting Florida Scrub Jay breeders relative to day in their nest cycles.

of one approximates the average daily molt rate when remex score is plotted against day in the nest cycle (Fig. 8). Using this rate, we conclude that females do not begin molt before their eggs hatch, even with late clutches, but that their mates regularly do so, and that some males begin molt even before the last eggs are laid. Four females molted while nesting. One already had dropped her first primary when captured on 28 May 1973; her young fledged on 7 June. Another, who had dropped the first primary by 1 June, fledged young on 8 June. Two other females had primaries 1 and 2 partially grown on 5 June and 14 June; their young fledged on 9 June and 20 June, respectively. Obviously, explanations for the

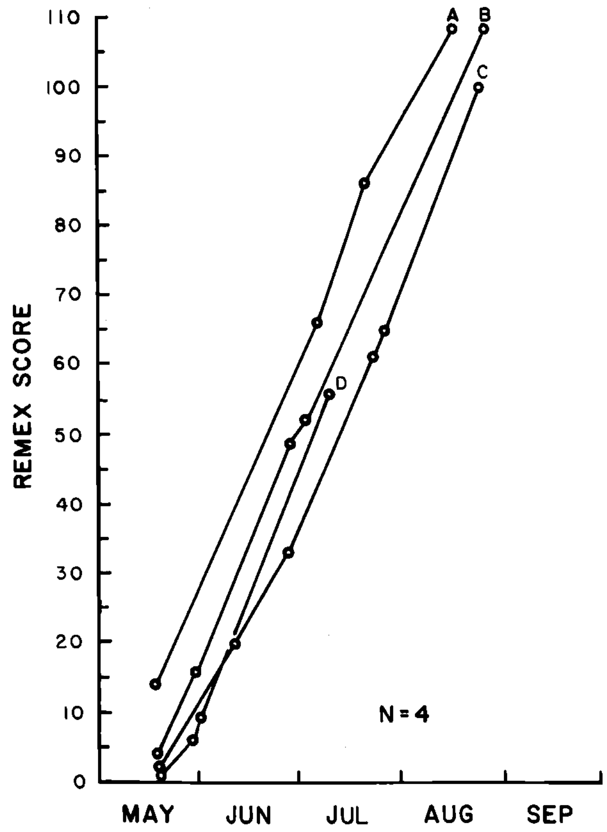

Fig. 9. Remex scores for four breeding male Florida Scrub Jays (A, B, C, D) examined four to six times during one definitive prebasic molt. A change in the slope of a line through time indicates a change in rate of molt.

timing of molt relative to breeding need to account for the differences in the timing of molt that exist between the sexes of *known breeders*.

Breeding males may begin molt while they are nesting, but they also may molt more slowly at this time. A consideration of chronological sequences of remex scores taken from four breeding male Scrub Jays illustrates this (Fig. 9). Three of the Jays (A, B, and C) were three years old; the fourth (D) was six years old. Males A and B finished nesting before mid-May; males C and D finished nesting after 1 June, their young fledging on 20 June and 2 June, respectively. After nesting, males C and D increased their rates of molt over the rates during nesting. The remex score of male C increased only 31 points in 39 days for a rate of 0.79 points per day during nesting, but then increased another 67 points in 58 more days for a rate of 1.16 points per day after his young fledged. The remex score of male D increased only 8 points in 12 days for a rate of 0.67 points per day during nesting, but then increased another 47 points in 40 more days for a rate of 1.175 points per day after his young fledged.

TABLE 11

Percentage of Juvenile Florida Blue Jays Examined in Successive Half-months Molting Feathers in Various Regions During the First Prebasic Molt

	June		July		Aug.		Sept.		Oct.	
No. jays	1 (1)	2 (18)	1 (16)	2 (27)	1 (24)	2 (27)	1 (9)	2 (13)	1 (4)	2 (4)
Primaries	0	0	0	0	0	0	0	0	0	0
Secondaries	0	0	0	0	54	78	89	62	0	0
Rectrices	0	0	0	4	75	78	78	69	0	50
Upper greater primary coverts	0	0	0	0	0	0	0	0	0	0
Upper middle primary coverts	0	0	0	19	54	30	0	0	0	0
Upper greater secondary coverts	0	0	0	33	92	70	0	8	0	25
Upper middle secondary coverts	0	33	19	70	46	22	22	23	0	0
Lower greater primary coverts	0	0	0	0	4	0	11	0	0	0
Lower lesser primary coverts	0	0	0	7	42	22	0	23	0	0
Lower secondary coverts	0	6	0	52	79	89	33	69	0	0
Marginal coverts	100	33	44	74	100	78	33	54	0	0
Alulae	0	0	0	0	0	4	11	0	0	0
Upper tail coverts	0	6	6	26	96	89	44	31	50	25
Lower tail coverts	0	0	19	67	96	100	67	62	0	25
Capital: forehead	0	0	0	0	8	85	67	31	0	50
crown	0	0	0	0	8	89	78	54	0	25
nape	0	0	0	0	8	78	78	23	25	25
lores	0	0	0	0	8	89	0	8	0	0
auricular	0	0	0	0	8	81	89	31	0	25
Humeral	0	89	88	100	100	100	89	85	25	75
Femoral	0	50	63	78	100	100	100	100	100	100
Crural	100	11	25	59	96	96	67	38	0	0
Spinal: pelvic	0	94	88	89	100	96	100	77	75	50
dorsal	0	94	94	100	100	100	100	92	75	75
interscapular	100	94	94	100	100	100	100	92	25	50
cervical	0	11	19	22	75	96	78	54	0	50
Ventral: submalar	0	0	0	0	29	93	56	54	25	75
cervical	0	67	81	100	96	100	100	85	75	50
sternal	0	83	100	100	100	100	100	100	100	100
abdominal	0	17	13	26	92	93	89	54	100	75

BLUE JAY MOLTS

First Prebasic Molt

The first prebasic molt of Blue Jays in Florida is a partial molt that includes all body feathers, most of the alar and caudal tract coverts, a variable number of secondaries 7 through 10, and a variable number of rectrices (Table 11). No juvenile Blue Jays were examined that molted primaries or upper greater primary coverts, and only a few individuals replaced either the lower greater primary coverts or alulae. Probably these latter feathers were lost accidentally.

The onset of the first prebasic molt was marked by the loss of some marginal coverts and was followed quickly by molt of some feathers in the interscapular region of the spinal tract and the sternal region of the ventral tract. The single individual captured in the first half of June was growing marginal coverts and a few feathers in the interscapular region of the spinal tract and in the crural tract (Table 11). Most Blue Jays captured in late June had started spinal, ventral, and

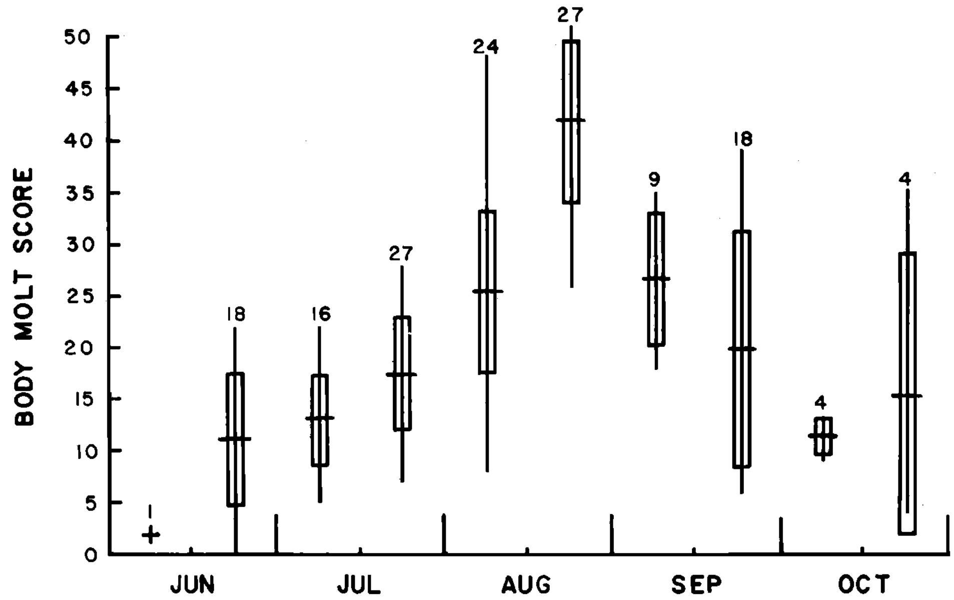

Fig. 10. Intensity of the first prebasic body molt of juvenile Florida Blue Jays examined in successive half-months. Intensity is described by the mean body score (horizontal line), range (vertical line), and one standard deviation on either side of the mean (rectangle). Numbers above ranges are sample sizes.

humeral tract molt, and all jays captured in early July were molting. The first Blue Jays with capital tract molt were captured in early August when two of 24 had started. By the second half of August, 26 of 27 Blue Jays examined had started capital tract molt. All feathers of the capital tract are dropped quickly, resulting in a short period when juvenile Blue Jays are virtually bald. Of four individuals captured in late September two had not started capital tract molt, while in two others it was almost completed. Some Blue Jays had dropped all juvenal body feathers by late September and had feathers growing in most body tracts. Three of the four juvenile Blue Jays captured in late October had almost finished growth of the first basic plumage; the fourth had extensive molt on all body tracts. As this same individual had not started capital tract molt when captured in late September, it may have been from a late brood. Although this individual had replaced all upper middle secondary coverts by late October, it had not replaced any juvenal secondaries or rectrices and had replaced only one upper greater secondary covert. All other Blue Jays captured after 1 September had replaced all upper greater and middle secondary coverts.

The mean body molt intensity score peaked in late August when most individuals had dropped their capital tract feathers (Fig. 10). The somewhat high mean score in late October was caused by the single individual, probably from a late brood, that was at an earlier stage of molt than most juvenile Blue Jays.

Molt of the proximal secondaries was first recorded in early August when 13 of 24 jays examined had dropped some secondaries. Of 23 juveniles examined after 1 September, 21 had molted secondaries 7 through 10, and two also had molted secondary 6. We suspect that the two individuals that had not dropped any secondaries were from late broods because they had not started capital tract molt. One was captured a second time in late October and still had not molted any secondaries. No juveniles replaced any of the distal five secondaries, and most did not replace secondary 6.

The first juvenile Blue Jays showing normal rectrix molt were captured in early August when 18 of 24 had dropped at least the central pair. Of 23 jays examined after 1 September, 21 had replaced at least the central pair, 13 had molted additional rectrices, and eight had replaced all rectrices. Most juveniles replacing rectrices additional to the central pair showed a gradation in length of the growing rectrices, those nearest full length being central with progressively newer feathers to the outside. This suggests that this rectrix molt was normal rather than a result of accidental feather loss. The jays captured in September that had replaced no rectrices were the same two juveniles that had not replaced secondaries or started capital tract molt. One was captured again in late October and still had molted no rectrices.

Two Blue Jays banded as nestlings were captured five times during their first prebasic molt. Molt of marginal coverts and spinal and ventral tract feathers had begun by 65 to 75 days after hatching. Molt of femoral and humeral tract feathers began between 75 and 90 days after hatching, and molt of crural and capital tract feathers and upper greater and middle secondary coverts began between 100 and 110 days after hatching. The last capture was made when one individual was between 110 and 120 days old, at which time feathers in all body tracts, the proximal secondaries, and some tail feathers were growing, and regrowth of the secondary coverts was completed.

The first prebasic molt in Florida Blue Jays begins in June, and some individuals are almost finished by late October. Thus, the first prebasic molt appears to take from 140 to 170 days. Blue Jays from earlier broods apparently replaced more juvenal plumage than those from late broods. Juveniles from early broods replaced some rectrices, secondaries, and all upper greater secondary coverts. In contrast, juveniles from late broods replaced no secondaries or rectrices and only a few upper greater secondary coverts.

DEFINITIVE PREBASIC MOLT

PRIMARIES AND SECONDARIES

Remigial molt, which is symmetrical and typically marks the start of molt, begins with the loss of primary 1 in Blue Jays. However, four birds had some body molt before any primaries were dropped. Spinal tract molt but no remigial molt was seen on one female on 29 June and two jays of unknown sex on 4 and 30 June. The fourth bird, a female with a well-developed brood patch, had spinal and humeral tract molt but no remigial molt on 23 June and 1 July. Remigial molt starts between early June and mid-July and continues into October. The primaries are molted in sequence with from one to four growing simultaneously (Table 12). Secondaries 1 and 8 are dropped in quick succession when primaries 3 and 4 are growing. Either secondary 1 or 8 is dropped first. The remaining secondaries are dropped in the following sequence: 9, 2, 7, 3, 10, 4, 5, 6. As many as five secondaries may be growing simultaneously. Secondary 6 is the last to grow.

The mean number of primaries growing per wing increased to 3.5 at remex

TABLE 12

PERCENTAGE OF ADULT FLORIDA BLUE JAYS IN EACH REMEX STAGE OF THE DEFINITIVE PREBASIC MOLT REPLACING PRIMARIES AND SECONDARIES

		Remex stage¹											
	No. jays	1 (27)	2 (29)	3 (18)	4 (18)	5 (14)	6 (8)	7 (4)	8 (1)	9 (4)	10 (6)	11 (16)	11+ (19)
Primary	1	100	93	28	0	0	0	0	0	0	0	0	0
	2	67	100	56	0	0	0	0	0	0	0	0	0
	3	0	69	100	67	0	0	0	0	0	0	0	0
	4	0	0	39	100	71	13	0	0	0	0	0	0
	5	0	0	0	39	100	75	0	0	0	0	0	0
	6	0	0	0	0	57	100	100	0	0	0	0	0
	7	0	0	0	0	0	38	100	100	50	0	0	0
	8	0	0	0	0	0	0	100	100	100	83	0	0
	9	0	0	0	0	0	0	25	100	100	83	6	0
	10	0	0	0	0	0	0	0	100	100	100	13	0
Secondary	1	0	0	11	89	93	13	0	0	0	0	0	0
	2	0	0	0	0	43	100	75	0	0	0	0	0
	3	0	3	0	0	0	25	100	100	25	17	0	0
	4	0	0	0	0	0	0	50	100	100	100	0	0
	5	0	3	0	0	0	0	0	0	50	83	50	0
	6	0	0	0	0	0	0	0	0	0	50	100	0
	7	0	0	0	0	36	25	75	100	25	0	0	0
	8	0	3	11	61	79	25	0	0	0	0	6	0
	9	0	0	0	11	71	88	25	0	0	0	0	0
	10	0	0	0	0	0	0	75	100	50	67	0	0
Mean no. growing													
Primaries		1.6	2.6	2.2	2.1	2.3	2.3	3.3	4.0	3.5	2.7	0.2	0.0
Secondaries		0.0	0.1	0.2	1.6	3.2	2.8	4.0	4.0	2.5	3.2	1.5	0.0

¹ Determined as described in footnote, Table 3.

stage 9 and then decreased (Table 12). The high value of 4.0 for primaries growing in remex stage 8 probably resulted from a small sample size. The mean number of secondaries growing per wing increased to 4.0 by remex stage 7 and then decreased after remex stage 8. The highest average number of growing remiges (eight) per wing occurred at remex stage 8, but this too may be high because of a small sample size.

RECTRICES

Molt of the rectrices begins with the dropping of the central rectrices and progresses centrifugally (Table 13). One of 14 birds with primary 4 growing and 13 of 14 birds with primary 5 growing had begun tail molt. Rectrices were molted in quick succession, so some individuals had the outer pair growing by remex stage 7. Typically all rectrices are fully grown by the time secondary 6 is fully grown. Frequently tail feathers are lost accidentally, and all tail molt recorded during remex stages 1 and 2, and some in a few later stages, may have been adventitious (Table 13). This is strongly suggested by the asymmetry of rectrix replacement in early stages.

As many as 10 rectrices may grow simultaneously. The mean number growing increased to 7.5 by remex stage 7 (Table 13). The high value of eight rectrices growing during remex stage 8 may be an artifact of the sample size of one. The

TABLE 13

Percentage of Adult Florida Blue Jays in Each Remex Stage of the Definitive Prebasic Molt Replacing Rectrices

		Remex stage[1]											
	No. jays	1 (27)	2 (29)	3 (18)	4 (18)	5 (14)	6 (8)	7 (4)	8 (1)	9 (4)	10 (6)	11 (15)	11+ (10)
Rectrix													
Left	6	0	7	0	0	0	0	100	100	100	100	13	20
	5	0	0	0	6	7	13	100	100	75	33	0	10
	4	0	0	0	6	21	50	100	100	25	17	0	10
	3	0	0	0	0	21	88	75	100	0	17	0	0
	2	4	7	0	17	86	100	25	0	0	0	7	0
	1	4	7	6	39	100	100	0	0	0	0	7	10
Right	1	4	3	6	33	100	88	25	0	0	0	0	0
	2	7	3	6	28	93	88	50	0	0	17	0	0
	3	7	0	6	6	36	100	75	100	0	17	0	10
	4	7	0	6	0	21	50	75	100	25	17	0	10
	5	4	0	0	0	0	0	75	100	75	50	0	10
	6	4	3	0	6	0	0	50	100	100	100	13	10
Mean no. growing		0.4	0.3	0.3	1.4	4.9	6.8	7.5	8.0	4.0	3.7	0.4	0.9

[1] Determined as described in footnote, Table 3.

mean number of rectrices growing decreases after remex stage 8. The largest number of rectrices and remiges growing simultaneously occurs during remex stages 7 and 8.

Body Feathers, Alulae, and Coverts

Table 14 gives the percentage of adult Blue Jays in each remex stage that have feathers growing in each of the areas examined. The upper greater primary coverts were molted with their corresponding primaries. Molt of the marginal, upper secondary, and lower wing coverts began with the onset of secondary molt and finished about the same time the primaries finished growing. In some individuals, humeral, femoral, spinal, and ventral tract molt started soon after loss of the first primary, and all of 19 birds examined with primary 3 growing had some body molt. Alula and capital tract molt started between the loss of primaries 7 and 10. Regrowth of the body tracts, especially the spinal and ventral tracts, extended beyond completion of remex growth. Molt of the tail coverts occasionally began with loss of primary 1. All birds were molting the tail coverts when the rectrices began molting. Occasionally regrowth of the tail coverts extended beyond completion of rectrix growth.

The intensity of body molt increased to a plateau between remex stages 5 and 9 and then declined (Fig. 11). Peak replacement of body feathers occurred when the greatest number of remiges and rectrices were growing.

Duration of Molt

We plotted remex scores for individual Blue Jays caught more than once against date (Fig. 12). Changes in the slopes of the lines connecting these points for an individual reflect changes in molt rate. Using recapture data, we calculated a

TABLE 14

PERCENTAGE OF ADULT FLORIDA BLUE JAYS IN EACH REMEX STAGE OF THE DEFINITIVE PREBASIC MOLT REPLACING BODY FEATHERS, ALULAE, AND COVERTS

	Remex stage[1]											
	1	2	3	4	5	6	7	8	9	10	11	11+
No. jays	(23)	(28)	(17)	(17)	(14)	(8)	(4)	(1)	(4)	(6)	(16)	(10)
Upper greater primary coverts	78	100	100	100	100	100	100	100	0	0	0	0
Upper greater secondary coverts	0	14	29	82	50	13	0	0	0	0	0	0
Upper middle secondary coverts	0	7	29	88	86	63	25	0	0	0	0	0
Lower primary coverts	0	0	18	12	50	100	100	100	50	83	0	0
Lower secondary coverts	4	7	24	82	93	100	100	100	50	33	6	0
Marginal coverts	13	68	71	100	100	88	50	0	0	17	6	0
Alulae	0	0	0	0	0	13	25	100	75	50	0	0
Capital tract	0	0	0	0	0	25	25	100	100	83	38	20
Humeral tract	30	71	71	100	100	100	100	100	100	100	50	20
Femoral tract	4	32	29	76	100	100	100	100	100	100	94	80
Crural tract	13	36	35	88	100	100	100	100	75	50	13	10
Spinal tract	65	96	88	100	100	100	100	100	100	100	100	60
Ventral tract	52	82	82	100	100	100	100	100	100	100	100	80
Upper tail coverts	4	21	29	76	100	88	75	100	25	17	6	0
Lower tail coverts	13	29	41	82	100	100	100	100	75	50	13	10

[1] Determined as described in footnote, Table 3.

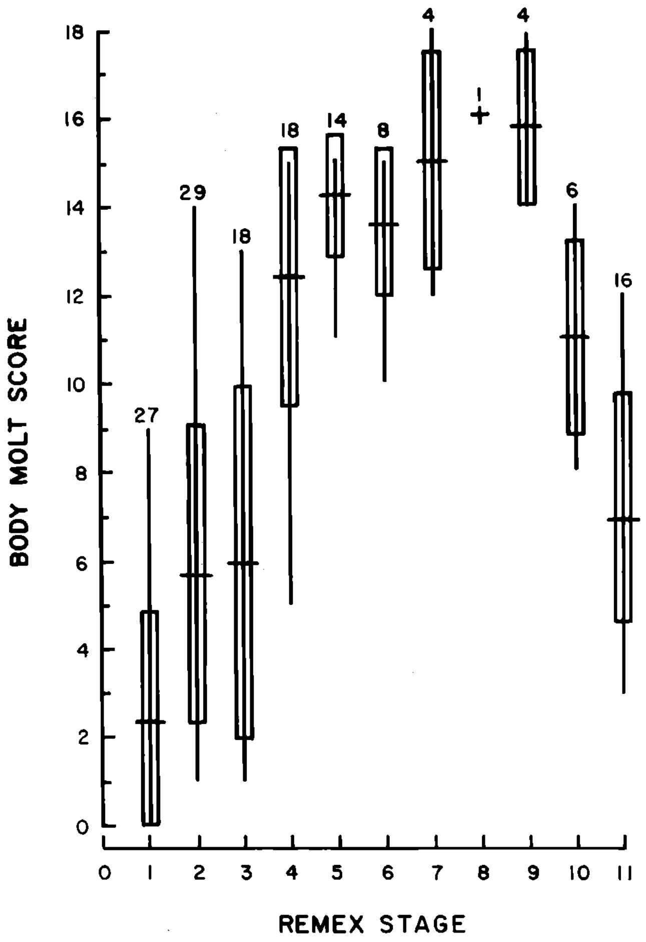

Fig. 11. Intensity of body molt for adult Florida Blue Jays examined during different remex stages of the definitive prebasic molt. Intensity is described by the mean body score (horizontal line), range (vertical line), and one standard deviation on either side of the mean (rectangle). Numbers above ranges are sample sizes.

mean increase of 0.86 points per day (s.d. = 0.11, range = 0.79–1.03, n = 4) for breeding females and 1.03 points per day (s.d. = 0.16, range = 0.80–1.39, n = 13) for unsexed yearling and older jays of unknown breeding status. These rates are not significantly different (*t* = 1.89, d.f. = 15, *P* > 0.05), so a mean molt rate of 1.0 point per day (s.d. = 9.17, range = 0.79–1.39, n = 17) was calculated for the total sample. At this rate remex molt would be completed in 110 days. If either of the extreme rates were maintained, remex molt would take 80 or 138 days.

The only two individuals captured more than twice were recaptured two times near the end of remigial molt. Because fewer remiges grow at this time, both showed a drastic decrease in their rate of molt.

Regression analysis of remex scores against date for all jays in active remigial molt produced rates similar to those calculated from recapture data. We calcu-

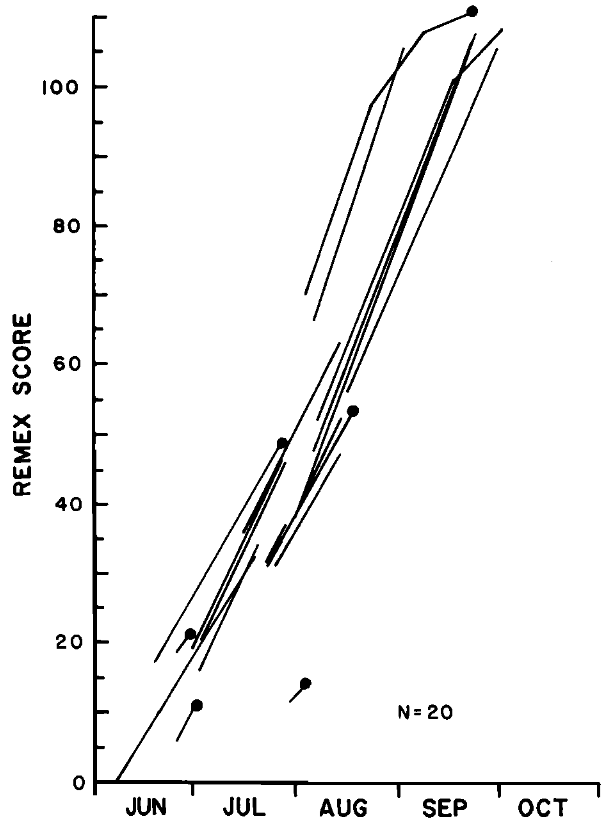

Fig. 12. Remex scores for 20 adult Florida Blue Jays examined two or more times during one definitive prebasic molt. Dots distinguish six breeding females from 14 individuals whose sex and breeding status are unknown.

lated a rate of 1.13 points per day (s.d. = 0.000803, n = 36) for breeding females, and a rate of 1.00 points per day (s.d. = 0.000078, n = 115) for the unsexed jays of unknown breeding status. These two rates are not significantly different (F = 2.33; d.f. = 1, 147; $P > 0.05$). Based on these calculations, Blue Jays seem to require an average of ca. 100 to 120 days to complete remigial molt.

CHRONOLOGY OF MOLT

The onset of molt for yearling and older Blue Jays is relatively synchronized. Most individuals had begun molting by the end of June, and all birds examined in the second half of July were molting (Table 15). Of 55 jays captured in late June, 45 (82%) were molting remiges. If remex score increases 1.0 point per day, then some individuals must have begun molting in early June, although none of the six captured then was molting remiges. Generally, adult Blue Jays begin molting between early June and mid-July with most individuals beginning in June. The progression of molt in the population can be illustrated by plotting remex scores against date for known yearlings, breeding females, and individuals of unknown sex and breeding status (Fig. 13). The capital tract and alulae start to

TABLE 15

PERCENTAGE OF ADULT FLORIDA BLUE JAYS EXAMINED IN SUCCESSIVE HALF-MONTHS MOLTING FEATHERS IN VARIOUS REGIONS DURING THE DEFINITIVE PREBASIC MOLT

	May		June		July		Aug.		Sept.		Oct.		Nov.	
No. jays	1 (18)	2 (1)	1 (6)	2 (56)	1 (21)	2 (27)	1 (16)	2 (7)	1 (5)	2 (10)	1 (13)	2 (4)	1 (1)	2
Primaries	0	0	0	80	95	100	100	100	60	50	15	0	0	
Secondaries	0	0	0	4	29	89	81	100	100	80	69	25	0	
Rectrices	0	0	0	14	19	74	75	100	60	70	15	25	0	
Upper greater primary coverts	—[1]	0	0	70	90	100	94	57	0	0	0	0	0	
Upper greater secondary coverts	—	0	0	4	29	78	13	0	0	0	0	0	0	
Upper middle secondary coverts	—	0	0	7	10	93	56	0	0	0	0	0	0	
Lower primary coverts	—	0	0	4	5	30	63	100	60	10	0	0	0	
Lower secondary coverts	—	0	0	4	29	81	81	86	40	10	0	0	0	
Marginal coverts	—	0	0	30	76	100	81	29	0	10	0	0	0	
Alulae	—	0	0	0	0	0	6	71	40	0	8	0	0	
Capital tract	0	0	0	0	0	0	6	86	100	60	23	0	0	
Humeral tract	0	0	0	39	86	100	88	100	80	80	31	25	0	
Femoral tract	0	0	0	13	38	85	81	100	100	100	85	75	100	
Crural tract	0	0	0	16	43	96	81	71	40	30	23	0	0	
Spinal tract	0	0	17	70	95	100	94	100	100	90	85	75	100	
Ventral tract	0	0	0	50	90	100	94	100	100	100	92	75	100	
Upper tail coverts	—	0	0	11	29	85	75	43	40	0	8	0	0	
Lower tail coverts	—	0	0	18	48	78	88	86	80	10	15	0	0	

[1] Dash = no data available.

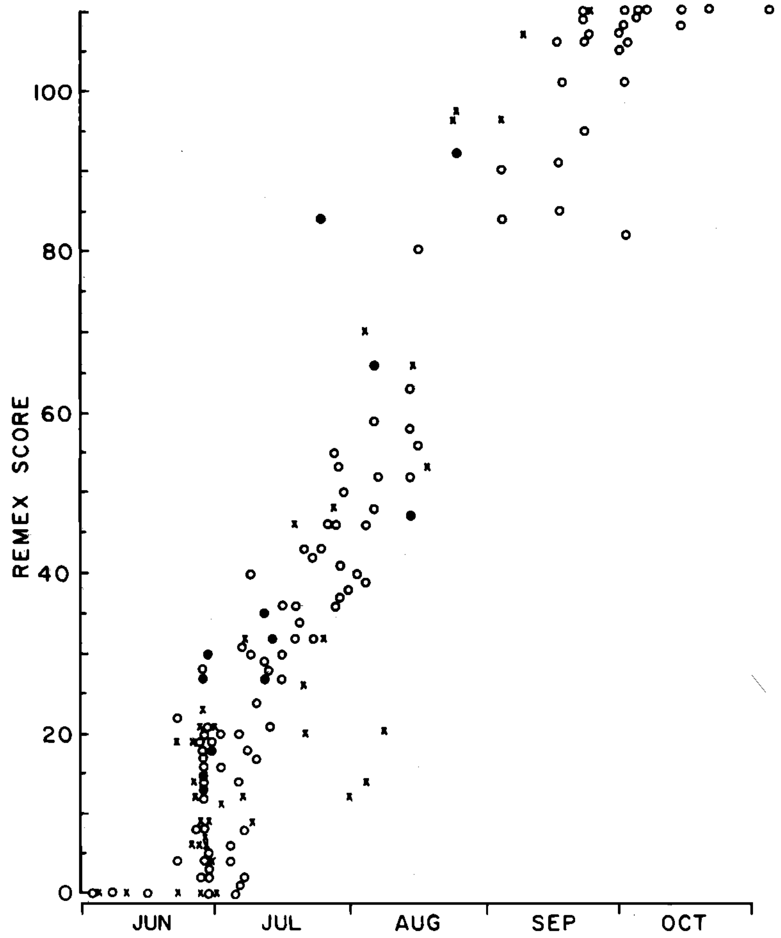

Fig. 13. Remex scores for adult Florida Blue Jays examined during definitive prebasic molt. Three classes are distinguished: unknown sex and unknown breeding status (open circles), breeding females (X), yearlings (closed circles).

molt later than all of the other feather groups. Molt was first recorded in these two tracts in early August. Some birds had begun molt in all other feather tracts by early July (Table 15). Some jays had completed remigial molt by late September, and all had finished by the first half of November. All had dropped all old body feathers by late October, and some birds still had feathers growing in the femoral, spinal, and ventral tracts in the first half of November. None of the seven Blue Jays in the Carnegie Museum of Natural History that were collected in Florida in November and December was growing any feathers.

Seventeen banded Blue Jays, of which four hatched in 1976 and 13 in earlier years, were captured on 28–30 June 1977. Using these samples, we calculated mean remex scores for yearlings and for older jays to determine if individuals entering their first complete molt tended to begin molting earlier than older individuals. Yearlings had a mean remex score of 22.0 (s.d. = 7.9, range = 13–30,

TABLE 16

PERCENTAGE OF ADULT FLORIDA BLUE JAYS EXAMINED IN SUCCESSIVE HALF-MONTHS THAT HAD STARTED THE DEFINITIVE PREBASIC MOLT

	June				July			
	1		2		1		2	
Class	n	%	n	%	n	%	n	%
Unknown sex and breeding status	4	0	35	86	23	96	24	100
Female breeder	2	0	21	71	5	80	3	100

n = 4), which was significantly higher ($t = 2.59$, d.f. = 15, $P < 0.05$) than the 9.5 (s.d. = 8.6, range = 13–30, n = 13) of older jays. This suggests that yearlings begin molting earlier than older individuals. However, some older Blue Jays had higher remex scores than some yearlings, which shows that overlap exists in the onset of molt between these two age classes.

Table 16 gives the percentage of breeding females and yearling or older unsexed jays of unknown breeding status that were molting in early and late June and July. Most individuals of both classes had begun molting by the end of June, although some individuals of both classes were not molting until late July. A 2 × 2 contingency test shows that equal proportions of breeding females and unsexed jays were molting in late June ($\chi^2 = 0.92$, $P > 0.25$). In all, 44 adult Blue Jays were examined on 28–30 June 1977. The mean remex score for females, 6.9 (s.d. = 7.2, range = 0–23, n = 16), did not differ significantly from the mean remex score of 11.2 (s.d. = 8.9, range = 0–30, n = 28) calculated for unsexed jays of unknown breeding status ($t = 1.70$, d.f. = 42, $P > 0.05$). Based on these data, breeding females and unsexed jays of unknown breeding status seem to begin molting at the same time. However, the exact breeding status of individual jays was not known; consequently, it was not possible to separate those that had finished nesting from those that still had active nests. The separation of breeding jays into these two categories may show that Blue Jays with active nests delay the onset of molt as do breeding female Scrub Jays.

Blue Jays in Florida nest from March until August. Thus, their nesting season is 50% longer than that of the sympatric Florida Scrub Jay for which we have no nest records past June. Dates of 69 Blue Jay egg clutches from Florida (Bent 1946) extend from 17 March to 29 August. If the late August clutch fledged young, nesting would have extended well into September. At Orlando, which is near the center of peninsular Florida and only 145 km north of Archbold Station, Nicholson (*in* Howell 1932) collected several sets of eggs and saw other occupied nests on 23 July (1910).

Blue Jays in Florida probably are regularly multibrooded (Howell 1932, Bent 1946), which contrasts with Florida Scrub Jays, where only 13% of the pairs attempt second broods (Woolfenden, unpubl. data). A five to six month nesting cycle in Florida allows ample time for Blue Jays to produce three broods. Based on intensive study of nesting in suburban Pinellas County, Florida, Woolfenden and Rohwer (1969) concluded that Blue Jays were multibrooded, with a major nesting peak in April and a smaller peak in early July.

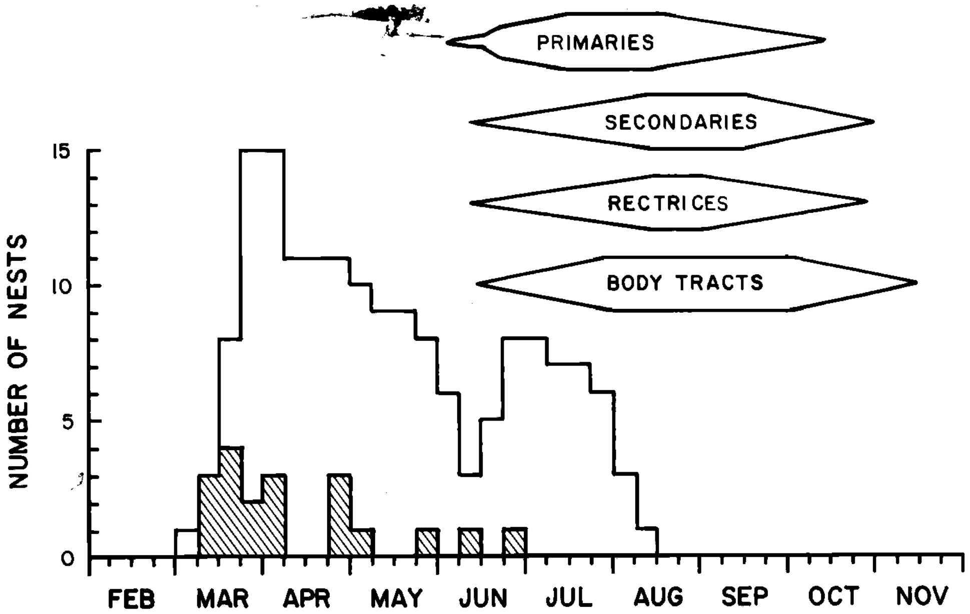

Fig. 14. The timing of breeding and the definitive prebasic molt in Florida Blue Jays. Four regions of the plumage are distinguished. The width of the bar for each region indicates the proportion of birds molting those feathers. When a bar is at maximum width, all birds were molting those feathers. Number of active nests per week (open area), and week of completion of clutches (hatched area) are shown by the histogram.

We assume that nesting schedules for Blue Jays at the Archbold Biological Station are similar to those reported for Blue Jays breeding elsewhere in central peninsular Florida. Limited evidence supports this decision. In 1976, when Bancroft obtained most of the detailed molt data, recently fledged Blue Jays were seen through early July. More importantly, two females he caught in early August had well-developed brood patches, which suggests some nesting extended at least that late (Bailey 1952, 1955). In addition, at least some Blue Jays at Archbold Station have active nests in September, more than two months later than the latest active Scrub Jay nest records. On 17 September 1980, Barbara C. Kittleson collected the remains of a freshly killed Blue Jay whose age we estimate as 25 ± 3 days, based on remigial development (remiges ca. one-quarter sheathed, primary 7 total length 60 mm, sheath 15 mm). Certainly this jay spent two to three of its three or four weeks post-hatching as a nestling.

We compared the chronology of nesting by Florida Blue Jays, based on the population breeding in suburban Pinellas County (Woolfenden and Rohwer 1969), with the timing of molt in 1976–77 at Archbold Station (Fig. 14). We considered the total number of nests active each week and the completion dates of 19 clutches, and molt of primaries, secondaries, rectrices, and body tracts.

The data show (Fig. 14) that for peninsular Florida Blue Jays, *as a population,* molt and breeding do overlap. Molt begins in late June, several weeks after the early April first peak of nesting, but at least two weeks before the early July second nesting peak. At Archbold Station all yearling or older jays examined after the first week in July were molting. Unfortunately, we do not know the exact breeding status of any individuals examined. Our best evidence of true overlap of molt with breeding comes from the two females Bancroft captured in early August that had well-developed brood patches. One had dropped the first two primaries, the other the first three primaries. However, their remex scores were 30 to 40 points behind average, suggesting they had delayed or were protracting molt. The chronologies of the entire central peninsular Florida population probably would suggest much less overlap if the non-breeders and those jays that stop breeding after only one nesting attempt were deleted from the samples.

COST CURVES FOR MOLT BY JAYS IN FLORIDA

Estimates of the energy and time required for molt are useful when assessing the importance of molt in the annual cycle of birds. The energetic cost of molt consists of the energy bound up in the feathers grown, the energy required to grow these feathers, and the energy required to meet additional thermoregulatory demands during their growth (Newton 1968b; Gavrilov and Dolnik 1974; Kendeigh et al. 1977; Dolnik and Gavrilov 1979). The caloric content of feathers and the cost of feather growth can be calculated from the weight of the new plumage (Kendeigh et al. 1977). Plumage functions to reduce body heat loss at low ambient temperatures or to reduce solar insolation at high ambient temperatures. Ambient temperatures at the Archbold Station during the time of jay molt usually range in degrees centrigrade from the twenties to the mid-thirties. The lower critical ambient temperature for birds the weight of these jays is about 18°C or 19°C (Kendeigh 1969; Calder and King 1974; Kendeigh et al. 1977). Therefore, the common problem during molt for these jays is not keeping warm but dissipating excess heat. We were unable to estimate the energy required for thermoregulation; therefore, the energy-expenditure curves we have constructed (Fig. 15) include only the costs of feather growth.

Dolnik and Gavrilov (1974, 1979, 1980) developed a method of estimating the rate of plumage synthesis from molt scores. We used a similar procedure but with certain differences. Dolnik and Gavrilov estimated that the energetic cost of growing an individual feather is higher during the pin stage and lower through the brush stage. Because of our method of scoring, we assumed a constant rate of keratin synthesis throughout the growth of feathers. This procedure may shift the peak in the energy cost curve slightly later in molt.

For 14 half-month periods (early May–late October) we calculated a mean molt score separately for primaries, secondaries, rectrices, and body feathers. For the primaries, secondaries, and rectrices, we next calculated the change in molt scores between half-month periods. The change in molt scores for each feather group was used to estimate the percent of those feathers grown during that time period. Values for primaries, secondaries, and rectrices were calculated only for adults, as juveniles molt only a few wing and tail feathers. We ignored flight feather molt in our calculations for juveniles. For body tracts we estimated the percentage of molt occurring in each time period from a graph of molt scores at each time period.

Three sources of information are available for estimating the weight of the

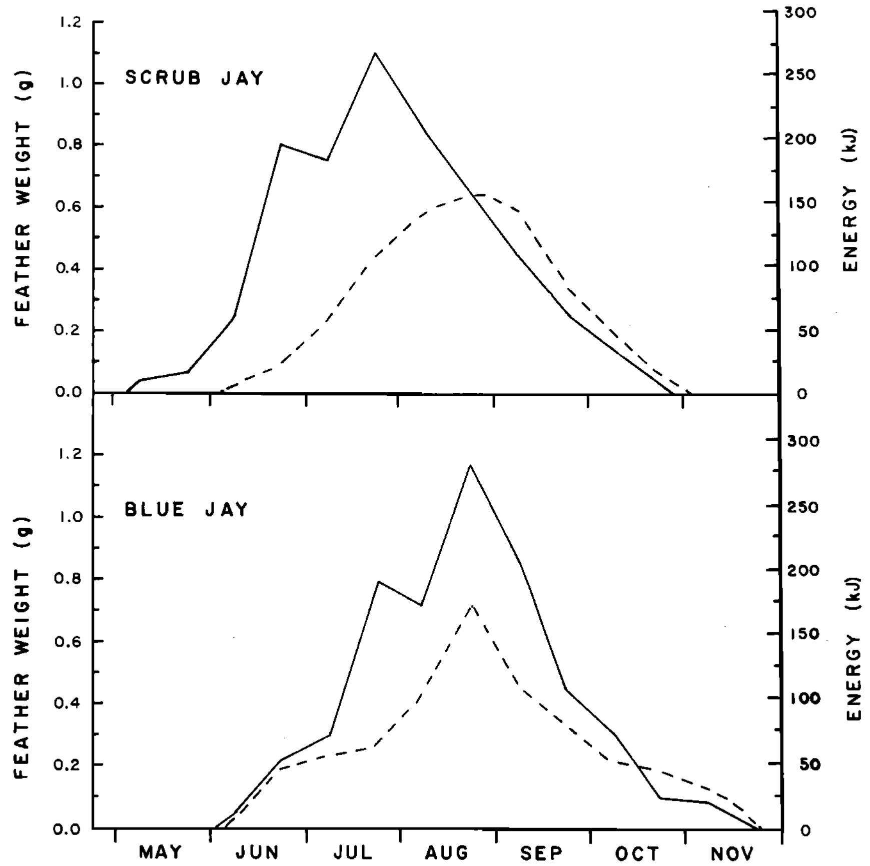

Fig. 15. Molt cost curves for Scrub Jays and Blue Jays in Florida. Solid lines represent the definitive prebasic molt, dashed lines the first prebasic molt. (See text for explanation.)

feathers carried by Scrub Jays and Blue Jays. Seel (1976) meticulously weighed numerous groups of feathers for sizeable samples of five British corvids, including the European Jay (*Garrulus glandarius*). Turček (1966) developed a formula for passerines in general that estimates weight of the entire feather coat from the weight of the bird. Pitelka (1958) weighed the flight feathers and body plumage of 20 Steller's Jays (*Cyanocitta stelleri*). Our results using these three sources were similar, ranging from 5.5 to 6.1 g for total feather weight for Scrub Jays and 5.2 to 5.8 g for Blue Jays. We used the estimates of 6.1 and 5.8 g derived from Seel's data because only he used feather groups that we could match with certain of our molt data.

Scrub Jay adults weigh 79.2 g, and juveniles, 75.0 g (Woolfenden 1978). Blue Jay adults weigh 75.5 g (Woolfenden 1974), and juveniles, 75.0 g (based on weights of 76 juveniles captured at Archbold Station, June–August 1976).

From Seel's data on male European Jays we obtained percentages of total body weight made up by feathers from our feather groups. Our four groups constituted 88% of all feathers on European Jays. Using these percentages and the body weights for the two jay species in Florida, we calculated weights for the same four feather groups. Using these weights and our estimates of the percentage of feather growth in each time period, we estimated the grams of feather keratin grown during each half-month time interval.

We emphasize that these calculations are based on a long series of estimates and should not be used beyond their accuracy. If the procedure seems worthwhile, the various steps can be repeated more accurately, for example, by following the molt histories of individuals instead of populations as we do in this section.

The weight of new feathers grown by adult Scrub Jays increases through late June, declines slightly in early July, and then peaks in late July. The decline in rate of accumulation of new feather tissue in early July is caused by a decrease in the growth rate of primaries and secondaries. At peak production in late July, adult Scrub Jays renew about 1.2 g of feathers per half-month. Juvenile Scrub Jays reach their maximum rate of feather growth in late August when they accumulate 0.65 g of feathers per half-month, approximately half of the maximum rate of adults. This is expected because the juveniles are not replacing most of the flight feathers. Adult Blue Jays show the same pattern of feather accumulation as adult Scrub Jays, but their peak occurs 1 month later, in late August. For juvenile Blue Jays the sharp peak in late August coincides with their rapid molt of head feathers. Their maximum rate of feather accumulation is about 0.7 g per half-month.

We estimated the net cost of feather synthesis from the weight of feathers produced. J. R. King (1980) calculated the heat of combustion of keratin to be 21.7 kJ/g. Direct measurements of the net efficiency of keratin synthesis show that it varies with food composition and temperature (Blackmore 1969; Kendeigh et al. 1977; Dolnik and Gavrilov 1979). According to Kendeigh et al. (1977), the energy cost of plumage replacement is 238 kJ/g of feathers on animal diet and 448 kJ/g on seeds. Using the first figure and our estimate of feather growth, we calculated that during the maximum rate of feather growth, the synthesis of feathers costs jays about 286 kJ per half-month period for adults and 167 kJ per half-month period for juveniles (Fig. 15).

From the equation of Kendeigh et al. (1977), we estimated an existence metabolism rate of 1860 kJ per half-month for adult Scrub Jays and 1800 kJ per half month for adult Blue Jays, and 1800 kJ per half-month for juveniles of both species. Our estimate for adult Blue Jays is considerably lower than the 2610 kJ per half-month period estimated for this species during the summer in Illinois (Clemans 1974). However, Blue Jays average 9 g heavier in Illinois than in Florida, and Clemans did not state whether or not his cost estimate included the cost of molt. Using our estimated cost of feather synthesis, we estimated the increase in metabolism necessary for feather synthesis. Even at maximum rates of feather synthesis, metabolic rates must increase only 15% to 16% for adults and about 9% for juveniles.

DISCUSSION

THE SCORING SYSTEM

Two methods are used for scoring molt when studying the rate and duration of molt. One system assigns birds to a stage of molt because of certain criteria of the new feathers (Pitelka 1945, 1958; Blyumental and Dolnik 1966; Dolnik and Blyumental 1967); the other assigns scores to certain individual feathers and then uses the sum of these scores as an index of the stage of molt (Evans 1966; Newton 1966; Ligon and White 1974). In order for either system to be linear, the molt increments used must require equal time intervals to be completed. The duration of molt will vary between birds if differences exist in the length of time required for an individual feather to grow, if variation occurs in the time interval between the loss of feathers, if fewer feathers are replaced during one molt cycle, or if the same feather is replaced more than once in the same molt cycle (Blyumental and Dolnik 1966; Evans 1966; Newton 1966; Blyumental et al. 1967; Blyumental 1973; Gavrilov and Dolnik 1974; Dolnik and Gavrilov 1974, 1979, 1980).

In order for our scoring system to be linear throughout an individual's molt cycle, individual feathers must take the same amount of time to grow regardless of their length, and they must be dropped at regular intervals so the same number of feathers is growing at any one time (Evans 1966; Newton 1966). The general pattern for passerines is that longer primaries, even though they grow faster, take slightly longer to complete growth than do shorter primaries (Evans 1966; Newton 1966; Dhondt 1973; Seel 1976). In contrast, King (1972) found in five captive Rufous-collared Sparrows (*Zonotrichia capensis*) that seven of their nine primaries grew to 60% of their total length in 8.6 to 9.4 days, whereas two of the longer primaries (4 and 5) took only 6.6 and 7.6 days to reach 60% of their total length. Dhondt (1973) reported that primaries are dropped at irregular intervals in captive Great Tits (*Parus major*). The first two primaries are dropped quickly, while the average interval between the loss of the other primaries varies from 5.3 to 12.0 days depending on the remiges involved. He also reported that the rate of increase in primary score varies with the period of molt, speeding up in the early stages and slowing down after the secondaries begin molting. Similarly, King (1972) found captive Rufous-collared Sparrows varied the interval between shedding successive primaries from 2.8 to 9.0 days. Newton (1966) also reported variation in the rate of molt for individual wild Bullfinches (*Pyrrhula pyrrhula*) caught more than twice during molt. Based on successive captures of the same individuals, he found that the fastest rate of remex molt was as much as three times the slowest. Between individuals, the fastest rate was as much as six times the slowest rate. Newton concluded that variation in rate of molt depends on the number of primaries growing because each primary takes about the same number of days to grow. The more primaries that are growing simultaneously, the faster the molt.

For the entire study population of Bullfinches, Newton (1966) found the average number of growing primaries remained between 2.8–3.0 throughout molt except for the beginning and end. For Redpolls (*Carduelis flammea*) Evans (1966) found no great variation in the number of primaries growing and concluded that the primaries are dropped at regular intervals.

The regression of molt score on date probably fits a sigmoid curve better than a straight line because only a few remiges are growing at the beginning and end of molt. However, the two times when only a few remiges are growing are short. Therefore, estimating the duration of molt based on a linear system will underestimate only slightly the actual duration of molt (Newton 1966). Seel's (1976) scoring system, which was based on the weight as well as the length of individual remiges, best fits a sigmoid curve. However, the curve had an extensive linear middle portion.

The linearity of the scoring system designed for this study is supported by several factors. The mean number of growing primaries for both jay species remains fairly constant throughout remex molt (Tables 3, 12). Several Scrub Jays captured three or more times maintained nearly constant molt rates (Table 7). Regression analysis of remex score on date accounts for 75% to 98% of the variation in remex score (Table 6). Therefore, we conclude that primaries are dropped at nearly regular intervals and that our molt scoring system is sufficiently linear to permit estimation of the duration of molt from rates of molt exhibited by individuals captured more than once and from regression analysis of remex scores for all jays caught in active molt.

First Prebasic Molt

Based on field work at Archbold Biological Station, the patterns of the incomplete first prebasic molt are similar for Scrub Jays and Blue Jays. Both species replaced all body feathers, but no primaries, greater primary coverts, or alula feathers. Both species molted between early June and November with peak intensity occurring between mid-July and late September. Both took between 140 and 170 days to complete the first prebasic molt, which is considerably longer than the 70 to 80 days reported for western Scrub Jays and Steller's Jays (Pitelka 1945, 1958). The major differences are that Blue Jays typically replaced more secondaries and rectrices than most Scrub Jays, and relative to the molt of other feathers, Blue Jays started capital tract molt later than Scrub Jays.

Juvenile Scrub Jays and Blue Jays normally replaced all marginal and secondary coverts. Certain southern, dry-region races of the Scrub Jay, *A. c. texana, cactophila,* and *hypoleuca,* also replace all secondary coverts, but the more northern races retain a variable number (Pitelka 1945). Some northern Blue Jays also retain juvenal secondary coverts (Pitelka 1946). A similar direct latitudinal trend in the retention of secondary coverts occurs in North American shrikes (*Lanius excubitor* and *L. ludovicianus,* Miller 1928, 1931) and certain northeastern European fringillids (Noskov 1975).

A few late-fledging Florida Blue Jays retained some upper greater secondary coverts. Similarly, Piñon Jays (*Gymnorhinus cyanocephalus*), Bullfinches, and Cardinals (*Cardinalis cardinalis*) from late broods retain more juvenal feathers than individuals from earlier broods (Ligon and White 1974; Newton 1966; and Wiseman 1977, respectively).

Young of both Scrub Jays and Blue Jays molted some proximal secondaries. Scrub Jays typically molted secondaries 9 and 10 with a few individuals molting secondary 8. No Scrub Jays molted secondaries 1–7. Most Blue Jays molted secondaries 7–10, and two individuals also molted secondary 6. No Blue Jays molted secondaries 1–5, and two individuals that we suspect were from late broods molted no secondaries at all. The only other races of the Scrub Jay known to replace secondaries are the southern *A. c. cactophila* and *hypoleuca,* with 12 of 41 specimens replacing some, and eight replacing all of secondaries 7 through 10 (Pitelka 1945).

All Scrub Jays and Blue Jays from Florida replaced the juvenal central rectrices, and some replaced the two rectrices immediately lateral to them. No Scrub Jays replaced additional rectrices, but eight of 23 Blue Jays examined late in molt replaced all their rectrices. Pitelka (1945) found only seven of 41 *A. c. cactophila* and *hypoleuca* replaced any rectrices, and three replaced all the rectrices. We suspect that in the latter cases the rectrices were accidentally lost. Five of nine northern Blue Jays in the Carnegie Museum of Natural History molted the central rectrices in the first prebasic molt, and one of these was molting rectrix 2 (K. C. Parkes, pers. comm.). All four not showing rectrix molt may have died before the molt started. Molt of the central rectrices probably is the prevailing pattern in Pennsylvania, and molt of rectrix 2 probably is unusual (K. C. Parkes, pers. comm.). Rectrices are excluded from the first prebasic molt in northern races of the Scrub Jay (Pitelka 1945), in the Steller's Jay (Pitelka 1958), fall-hatched Piñon Jays (Ligon and White 1974), Clark's Nutcrackers (*Nucifraga columbiana,* Mewaldt 1958), and some species of *Corvus* (Witherby 1913; Emlen 1936).

Juvenile Scrub Jays began capital tract molt when they were between 80 and 100 days old and soon after the onset of molt elsewhere on the body. Blue Jays delayed capital tract molt until shortly after 100 days of age, which was about a month after molt began elsewhere. Some young Scrub Jays began capital tract molt in late June; no Blue Jays were captured that had begun capital tract molt before early August.

In sharp contrast to young Scrub Jays whose head molt was gradual, young Blue Jays dropped their head feathers nearly simultaneously resulting in a short period when they appeared nearly bald. This striking bald appearance disappears in about a week because of growth of the new head feathers. It may be that delayed head molt in juveniles typifies only peninusular Florida populations, as we find no reference to naked-headed Blue Jays from elsewhere. No mention is made of near simultaneous head molt in the congeneric Steller's Jay either; however, Pitelka's (1958) study was made far north in the species' range.

We speculate that difference in their social systems may account for the differences we found in the timing of capital tract molt in juvenile Scrub Jays and Blue Jays in Florida. Following a relatively short breeding season, juvenile Scrub Jays form small troops that wander through the permanent territories of neighboring breeders. Prior to much prebasic molt, while they retain the overall appearance of the juvenal plumage, the young Scrub Jays meet with less immediate and less severe aggression from their neighbors than occurs once they take on the overall appearance of adults (Woolfenden and Fitzpatrick 1977). We assume a similar situation exists in Blue Jays. Furthermore, we assume that the elaborate and variable (Thompson and Caputo 1977) head markings of Blue Jays are important in social interactions. In Florida the nesting season for Blue Jays extends 2 months longer than for Scrub Jays. Juveniles produced early in a nesting season may reduce the aggression they receive from late breeders by delaying their head molt. Once nesting terminates, Blue Jay territoriality also ceases (Hardy 1961), and perhaps then it is advantageous for Blue Jays to resemble adults in order for them to establish a position in the loose aggregations they form. The sooner they achieve this appearance, the better off they may be. Farther north where nesting is less protracted, more time for head molt by juveniles may exist between breeding and flock formation.

DEFINITIVE PREBASIC MOLT

The renewal of Scrub Jay and Blue Jay primaries follows the descending sequence of other passerines, proximal to distal, P1 through P10 (Stresemann and Stresemann 1966). The secondaries are molted in two groups, distal (1–6) and proximal (7–10). Typically, the Scrub Jays we sampled began secondary molt with the loss of secondary 8; only occasionally was secondary 1 dropped before 8. Blue Jays began secondary molt with the loss of either secondary 1 or 8. Both species began secondary molt about the time primary 4 was dropped, and all were growing secondaries when primary 5 was growing. The pattern of remex molt for Florida Scrub Jays was the same as that exhibited by western Scrub Jays (Pitelka 1945) and Piñon Jays (Ligon and White 1974). In contrast, the larger Rook (*Corvus frugilegus*) and Clark's Nutcracker do not begin secondary molt until primary 5 is growing (Witherby 1913; Mewaldt 1958).

About the same time as primaries 4 or 5 were lost, both Scrub Jays and Blue Jays began tail molt by loosing the central rectrices. Tail molt progressed centrifugally and was complete at about the same time as remigial molt. This timing and sequence of remex and rectrix molt closely follows that of other corvids (Pitelka 1945; Ligon and White 1974; Seel 1976) and passerines in general (Dwight 1900; Jones 1930; Svensson 1975; Vinogradova et al. 1976).

Scrub Jays began body molt between the loss of primaries 3 and 5. Blue Jays began body molt relatively earlier, concurrent with the loss of primaries 1 and 2. All Blue Jays, but only 10% of the Scrub Jays, were in body molt when primary 3, but not 4, was growing. Because of the relative delay in the start of body molt for Scrub Jays, both species were in full body molt during July and August, the hottest months of the year in Florida. Several other corvids also molt their body plumage in midsummer, even though their primary molt may occur at some other time [western Scrub Jays, Pitelka 1945; Clark's Nutcracker, Mewaldt 1958; Carrion Crow (*Corvus corone*), Rook, Jackdaw (*C. monedula*), Black-billed Magpie (*Pica pica*), and European Jay, Seel 1976].

Most of the Scrub Jays and Blue Jays we examined required 3 to 4 months to complete remigial molt and possibly a few additional weeks to finish body tract molt. Pitelka (1945) found that various races of Scrub Jays in western North America take 3 to 4 months to complete the entire prebasic molt whereas Unicolored Jays (*Aphelocoma unicolor*) and Mexican Jays (*A. ultramarina*) take 4 to 5 and 4 to 6 months, respectively. Arnold (*in* Mewaldt 1958) found Blue Jays in New York in molt from June to October but gave no estimate of the time required for an individual to complete molt. Steller's Jays complete all molt in 2 to 2.5 months (Pitelka 1958), while Clark's Nutcrackers take 4.5 to 5 months to complete remigial molt, and from 8 to 9 months to complete all molt (Mewaldt 1958). We calculated from Ligon and White's (1974) work that Piñon Jays take 3.5 to 4.5 months to complete remigial molt.

Based on typical corvid molt patterns, we calculate that various species of *Corvus* in England take 3.5 to 6 months and Black-billed Magpies, European Jays and Choughs (*Pyrrhocorax pyrrhocorax*) take 3 to 4 months to complete remigial molt. All molt is completed 1 or 2 months later (Holyoak 1974; Seel 1976).

Most corvids take more time than other passerines to complete the definitive prebasic molt (Mewaldt 1958). However, certain non-migratory north-temperate passerines require about the same amount of time as Scrub Jays and Blue Jays (e.g., Great Tit, 3 months in Belgium, Dhondt 1973; Loggerhead Shrike, 3 months in western United States, Miller 1928; House Finch, *Carpodacus mexicanus*, 3 to 4 months in California, Michener and Michener 1940), whereas some migratory passerines complete molt in much less time. White-crowned Sparrows (*Zonotrichia leucophrys*) take less than 2 months in Alaska and California (Morton et al. 1969; Morton and Welton 1973), and some European finches take only 1.5 to 3 months (Evans 1966; Newton 1968a). Dolnik and Blyumental (1967) have shown a reduction in duration of molt with increasing migration distance in 10 eastern European species. A similar trend has been shown for sedentary and migratory subspecies of the Chaffinch (*Fringilla coelebs*) and House Sparrow (*Passer domesticus*; Dolnik and Gavrilov 1975) and latitudinal populations of Great Tits (Blyumental et al. 1967).

Scrub Jays began their definitive prebasic molt some time during a two-month period from mid-April to mid-June. Most Blue Jays began molting within a one-month period, mid-June to mid-July. The first Florida Scrub Jays to begin molting were non-breeding yearling jays of both sexes, which were starting their first complete molt. Older helpers and breeding males generally began molting during May; late-nesting females began molting last. Yearling Blue Jays began molting earlier than many older Blue Jays. Female Blue Jays appeared to begin molting at the same time as other Blue Jays, although some late-nesting females had remex scores considerably below average for the population, suggesting delayed or protracted molt.

Yearling corvids of other species also tend to begin molting earlier than older birds (Pitelka 1945, 1958; Mewaldt 1958; Holyoak 1974; Ligon and White 1974; Seel 1976). The general explanation is that yearling birds may not breed and that non-breeders can start molt earlier than breeders (Mewaldt 1958; Pitelka 1958; Holyoak 1974; Samson 1976; Seel 1976), possibly because of less inhibition of molt by reproductive hormones (Payne 1972; Ligon and White 1974). It may be that at least some Blue Jays breed in their first year in Florida, as two yearling females we caught had well-developed brood patches. Yearling Blue Jays have been reported breeding elsewhere in North America (Hickey 1952; Laskey 1958; Hardy 1961). In Cassin's Finch (*Carpodacus cassinii*), first-year males do not breed, and they begin molting earlier and take longer than breeding birds, whereas first-year females do breed, and they molt at the same time as older breeders (Samson 1976). Data are insufficient to determine if yearling Blue Jays that breed begin molting earlier than older, breeding Blue Jays.

Although most birds begin prebasic molt at the end of the breeding season when reproductive activities are completed (Payne 1972), Scrub Jays show variation related to breeding status and sex. The non-breeding helpers, including individuals several years old, began molting from late April through late May regardless of the nesting status of the pair with which they were associated. Breeding males followed the same schedule, although they did protract molt if still nesting (*see* also Snow and Snow 1964). In contrast, breeding females began molting in late May only if they were finished nesting, and delayed molt if nesting still was in progress. Only extremely late-breeding females began molting before their nests were empty.

Blue Jays began molt in mid-June or early July after most nesting activity had stopped. Some breeding female Blue Jays apparently delayed the onset of molt and perhaps protracted molt while still nesting. We did not determine the effect, if any, of late nesting on molt of breeding males. Two females with well-developed brood patches had started molt, suggesting molt and nesting do overlap at least occasionally. Holyoak (1974) and Seel (1976) postulate that different dates for the onset of molt in British corvids reflect their different breeding schedules. Our data for the two Florida jays support their conclusion. Individual Scrub Jays that finished nesting between late April and late June began molting between late April and mid-June. Blue Jay nesting in Florida often extends beyond June, and the jays did not begin molting until June or early July.

Most corvids begin molt after breeding (Pitelka 1945, 1958; Holyoak 1974; Ligon and White 1974; Seel 1976). Late-breeding individuals, however, may start molt while still attending active nests (Seel 1976). Exceptions are Clark's Nutcracker and the Common Raven (*Corvus corax*) which begin molting early in the breeding season and continue throughout the nesting cycle (Mewaldt 1958, Gwinner 1966). Typically, Piñon Jays breed in the spring (Balda and Bateman 1971, 1972) and molt thereafter (Ligon and White 1974). However, breeding also may occur during late summer or fall in response to food abundance (Ligon 1971, 1974). If breeding begins while molt is in progress, feather loss stops until breeding terminates (Ligon and White 1974).

INTERACTIONS OF MOLT AND BREEDING

Relationships between molt and breeding have been the subject of much recent discussion (Ricklefs 1974, and references therein). In most temperate zone small passerines, molt follows breeding with little overlap between them. Jays in Florida basically match this pattern, but with some intriguing variation associated with age and sex.

Reproductive hormone levels are known to inhibit the onset of molt in many birds (Payne 1972). However, many passerines, including several corvids, do molt and breed simultaneously (Mewaldt 1958; Gwinner 1966; Dolnik 1975). Endocrine control of molt appears to be a proximate mechanism for integrating the annual cycle. Several evolutionary hypotheses are available to explain why endocrines act to separate molt and breeding in temperate birds. Though not entirely exclusive, these explanations emphasize energy requirements, flying efficiency, temperature regulation, and water balance. We examined our data on molt and breeding in Florida Scrub Jays with knowledge of these hypotheses and the assumption that the timing is adaptive. Our data for Scrub Jays are extensive, but our data for Blue Jays are limited and therefore, unfortunately, have relevance to only some of this discussion.

The energy hypothesis is based on the assumption that both molt and breeding require large amounts of energy and that their concurrence stresses energy budgets (Payne 1972; Foster 1974, 1975). Differences in the timing of molt by different age and sex classes within the same species are explained by their different roles during reproduction. For many of the species in which yearlings do not breed, these young birds begin molt earlier than the breeders (Pitelka 1958; Samson 1976). For species in which one sex is free of reproductive responsibilities before the other, the emancipated sex regularly begins molt earlier and during the species' breeding season (e.g., tetraonids and anatids, King 1974). The usual explanation is that the energy saved by curtailing reproductive duties can be used for molting. Information on activities during nesting by Scrub Jays performing different reproductive roles permits an evaluation of this hypothesis as an explanation for the timing of molt in this population.

The subtropical breeding habitat of Florida Scrub Jays often is hot; rarely is it cold. Breeding females do all of the incubating and brooding, and they are very attentive (Stallcup and Woolfenden 1978). Females often stand over their nests, many of which are mostly exposed to the sun, and provide shade instead of heat. Even in more temperate climates incubating and brooding need not be particularly energy demanding. Recently, Walsberg and King (1978a, 1978b) showed for three species that the energy demands of the incubating females were less than for their mates who did not use the insulating benefits of their nests. However, several authors have suggested that some incubating birds increase their metabolic rates 25% to 30% above that used by a non-incubating bird in a nest (Drent 1973; Mertens 1977, 1980; Biebach 1981).

While breeding female Scrub Jays remain at their nests, their mates and any helpers that are present expend time (DeGange 1976), and therefore energy, foraging for food for the nestlings, and to some extent for the breeding females. From 57% to 100% of the food brought to nestlings is obtained by the breeding males and their helpers (Stallcup and Woolfenden 1978).

These observations suggest that in Florida Scrub Jays it is the breeding males and perhaps even the helpers, and not the breeding females, who are expending the greatest amount of energy during nesting. Regardless, we do know that it is the breeding males and the helpers who regularly overlap molt with breeding, and the females who delay molt and reduce overlap. Fragmentary data suggest that yearling Blue Jays molt earlier than older individuals, and that female breeders with late nests molt last.

Considerable energy is needed to replace the entire feather coat (King and Farner 1961; Dolnik 1971; Kendeigh et al. 1977), but a long molt probably is not energetically expensive on a daily basis (Payne 1972). The molt cost curves we obtained for Florida jays (Fig. 15) show that synthesis of new feathers does not reach a maximum until 2 months after the onset of molt and at least 1 month after breeding has stopped. At the maximum, daily metabolism might have to increase only as little as 15% in order to account for feather synthesis. If feather synthesis is most rapid during the first stages of feather growth (Dolnik and Gavrilov 1979), the peak in the cost curve would be shifted only slightly earlier in the season. We suspect that the energy hypothesis does not explain what we have found for Scrub Jays, especially, and for Blue Jays. Therefore, examination of other hypotheses seems warranted.

Maintenance of peak flying ability during certain seasons may select for the timing of molt (Stresemann and Stresemann 1966, Woolfenden 1974, Seel 1976). Assuming loss of flight feathers increases wing loading and decreases flying ability, we examine when in their annual cycle Scrub Jays fly most often and when they molt. Territorial defense, dispersal forays, and acorn harvesting appear to require the most flying (DeGange 1976; Woolfenden, pers. obs.). Defense (Barbour 1977) and dispersal peak biannually in early spring and early fall. Acorn harvesting also occurs in the fall. Molt, and especially remigial molt, occurs when these events are not taking place (Figs. 7, 14). Although these factors may have selected for the general timing of Florida Scrub Jay molt, we do not see that they are related to the differences exhibited by the sex and age classes. Blue Jays, which have a longer breeding season, molt later than Scrub Jays. Blue Jays also harvest acorns. However, they also have a lighter wing loading than Scrub Jays (Woolfenden 1974) and also may lack winter territories (Hardy 1961). These differences may allow for greater overlap between molt and acorn harvesting in this species.

Ability to regulate body temperature could select for timing of molt. Molting birds have more blood near the surface in the highly vascularized growing feathers (Payne 1972), and this can cause either greater heat loss or increased heat load depending on environmental conditions. Compared with non-molting birds, those in molt increase their metabolic rate in the thermoneutral range and increase the rate more at lower temperatures (Blackmore 1969; Lustick 1970; Dolnik and Gavrilov 1975, 1979). High solar radiation and high temperatures can lead quickly to hyperthermia and death for nestlings (Morton and Carey 1971; Ricklefs 1974). Furthermore, under hyperthermic conditions, growth rates of young may be reduced because energy is being diverted from growth to heat dissipation.

Late in the nesting season female Scrub Jays often stand over their nestlings with their feathers ruffled, their sparsely feathered carpals and shanks exposed, and panting. Females also face away from any breeze that may exist, which further ruffles their dorsal feather coat. The naked or partially feathered young often assume a neck-stretched cooling stance (Woolfenden 1978, color frontis) and pant.

By not molting while breeding, female Scrub Jays have their entire feather coat for protection from intense solar radiation, a function it is known to serve in other birds (Marder 1973; Thomas and Robin 1977). Loss of feathers decreases insulation, and growth of new feathers increases blood flow near the body surface. Blood heated at the surface and carried to the body core would increase further the possibility of hyperthermia (Calder and King 1974). Direct solar radiation can lower the upper critical temperature that can cause heat stress (Porter and Gates 1969). During molt, metabolic rates increase 238 kJ/g of feather grown (Kendeigh et al. 1977). Only 21.7 kJ of this is stored in each gram of new feathers. The difference between these two figures is the amount of energy that must be used in order to prevent increased heat load and possibly higher temperatures (Newton 1968b). Breeding males and helpers, who are not restricted to a nest, can move about more freely and use microhabitats and cooling behaviors unavailable to the brooding female and nestlings. Thus, selection may favor a separation of molt and breeding in female Florida Scrub Jays in order to decrease heat load.

Some of the same environmental factors that affect temperature regulation in birds also affect water balance. Birds pant in order to lower body temperature, and panting results in water loss (Calder and King 1974). During molt, water needs increase because blood volume increases and because relatively more blood is near the body surface where water loss is more rapid (Chilgren 1975; Chilgren and deGraw 1977; Dolnik and Gavrilov 1979). Florida Scrub Jays live in a xeric environment; however, molt occurs during summer when rainfall and humidity reach their peaks. Even under conditions of ample water, maintaining proper water balance in a hot environment can be stressing. The breeding female may use evaporative cooling more than her mate and helpers because she is restricted to the nest to shade her young from high solar radiation. Although water to drink may be available, the breeding female may not be able to drink regularly because she needs to remain at the nest to protect her young. Sometimes, even short absences could cause hyperthermia in the young (Morton and Carey 1971). By separating molt and breeding, nesting females may reduce their water stress. This argument is based on the assumption that either water or opportunities to obtain water are limited.

Assuming selection has determined the integration of molt in the annual cycle of the Florida Scrub Jay, it may be that the maintenance of good flying ability during peak times of territory defense, dispersal, and acorn harvesting, as well as breeding, determined the timing and duration of molt. Thermoregulatory or water balance problems or both may have determined the timing of molt among the different classes of jays.

ACKNOWLEDGMENTS

The facilities of the Archbold Biological Station were made available through the generosity of the late Richard Archbold and Dr. James N. Layne, Executive Director. Bancroft's field work was supported by a grant from the Frank M. Chapman Fund of the American Museum of Natural History, and through the kindness of his parents Barbara and George Bancroft. Ann M. Bancroft gave GTB invaluable encouragement, support, and help with all aspects of the project. This paper fulfilled part of the requirements for the Master of Arts in Zoology for GTB.

Kenneth C. Parkes made available specimens and information on specimens in the Carnegie Museum of Natural History. John W. Fitzpatrick, Fred E. Lohrer, and Chester E. Winegarner kindly helped with field work. Discussions with Warren G. Abrahamson, Mary H. Clench, Wayne Hoffman, Roy W. McDiarmid, Kenneth C. Parkes, G. Bruce Williamson, and numerous colleagues at the University of South Florida improved various aspects of this study. J. Steve Godley, Roy W. McDiarmid, Susan C. White-Schuler, and G. Bruce Williamson read and improved early drafts of the manuscript. Mary H. Clench, Mercedes S. Foster, James R. King, Martin L. Morton, Kenneth C. Parkes, and Frank A. Pitelka gave invaluable insight into improvements of later versions. V. R. Dolnik pointed out many Russian papers on molt and helped us immensely with our understanding of the energetics of molt. To all the above people and institutions we are extremely grateful.

SUMMARY

The pattern of molt by Scrub Jays and Blue Jays in Florida is similar to that exhibited by other passerines. During the first prebasic molt both species replace all the body feathers, but no primaries, greater primary coverts, or alula feathers. Both species molt between early June and November with peak intensity occurring between mid-July and late September. Both take between 140 and 170 days to complete molt. Scrub Jays typically replace secondaries 9 and 10 and occa-

sionally secondary 8. Blue Jays usually replace secondaries 7 through 10. Both typically replace the central pair of rectrices. Scrub Jays frequently replace the pair of rectrices immediately lateral to the central pair. Blue Jays occasionally replace all rectrices. Scrub Jays begin capital tract molt soon after the onset of molt, but Blue Jays delay it for approximately one month. Blue Jays drop all their capital tract feathers at once, resulting in a short period when they appear bald. We speculate that this difference in the timing of capital tract molt may be related to differences in their social systems.

The definitive prebasic molt starts with the loss of primary 1, and the primaries are molted in sequence, P1 through P10. Secondary and rectrix molt begins between the loss of primaries 3 and 5. The secondaries are molted in two groups: 1–6, and 7–10. Tail molt starts with the central pair and progresses centrifugally. Scrub Jays begin body molt between the loss of primaries 3 and 5, whereas Blue Jays begin body molt when primaries 1 and 2 are lost. Body molt occurs during the hottest months, July and August. Scrub Jays begin remex molt between late April and June, but Blue Jays delay the onset of remex molt until June or July.

The duration of Scrub Jay and Blue Jay remigial molt in Florida is relatively long, usually requiring 90 to 120 days. A few individuals may complete remigial molt in less than 90 days, and some may take longer than 120 days. Completion of growth of the body plumage may extend for several weeks beyond completion of remigial molt.

Individual Scrub Jays finish nesting from late April to mid-June. In Pinellas Co., Florida, Blue Jays typically nest into June with some nesting extending into August; the schedule appears to be the same at Archbold Biological Station in Highlands Co., Florida. Yearling Scrub Jays, regardless of sex, begin molting in late April to mid-May. Older helpers and breeding males begin molting in May. Breeding females begin molting between mid-May and late June. Helpers and breeding males begin molting regardless of the stage of their family nesting cycle, but breeding males may protract remigial molt. Breeding females delay molt until they are finished nesting, although extreme late-nesting females will begin molting before young fledge. Blue Jays begin molting in June to early July. Some evidence suggests that late-nesting female Blue Jays delay the onset of molt and probably protract remigial molt.

Relationships between molt and breeding have been the subject of much recent discussion. The pattern for most temperate-zone small passerines is breeding followed by molt with little overlap between them. Jays in Florida basically match this pattern, but with some intriguing variation associated with age and sex. Several hypotheses are available to explain why molt and breeding are separate in temperate birds. Though not entirely exclusive, these explanations emphasize energy requirements, flying efficiency, temperature regulation, and water balance. We examined our data on molt and breeding in Florida jays in light of these hypotheses and the assumption that the timing is adaptive.

Our estimates of the direct cost of feather replacement, albeit crude, and information on time budgets cause us to question energy requirements as the direct explanation for the separation of molt and breeding in these jays, and especially the Florida Scrub Jay. A combination of temperature and water regulation and perhaps flying efficiency seems more logical.

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