

## THE MOLT AND TESTIS CYCLES OF THE ANNA HUMMINGBIRD

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At the present time, there is virtually no information in the literature on hummingbirds concerning the relation of the reproductive cycle, molt cycle, and other physiological events to the occupation and defense of territory. Consequently, the associated displays, and their function and relation to territorial occupation, are at best only partly understood. Moreover, any analysis of behavior should include a study of environmental relations of the species throughout the year in conjunction with the sequence of events in the annual cycle (Pitelka, 1942:196).

Among North American hummingbirds, the Anna Hummingbird (*Calypte anna*) offers several advantages for a study of these problems. It is permanently resident in most of its range, being confined as a breeding species to the Upper Sonoran Zone of California west of the Sierra Nevada and of northwestern Baja California (Grinnell and Miller, 1944:219). Field observations can therefore be made at any time of the year in the various situations utilized by this species, and specimens can be collected regularly for the study of the molt and testis cycles. In addition, a number of specimens are available in collections, and the existing literature is perhaps more extensive for this hummingbird than for any other in North America.

The primary objective of this study was to correlate the timing of events in the annual cycle of the male, particularly molt and reproduction, with the complex territorial behavior shown by this species. In particular, information was gathered on the nature of the territory in the non-breeding season, since none of any consequence has yet been reported in the literature. Information on behavior and display of Anna Hummingbirds is to be presented at a later date (Williamson and Pitelka, MS).

## ACKNOWLEDGEMENTS

This study was conducted under the guidance of Frank A. Pitelka, to whom I am indebted for advice, counsel, and critical reading of the manuscript. Robert Rausch read the manuscript and offered many helpful suggestions. Alden H. Miller and Oliver P. Pearson very generously aided me in the study of the testis cycle. Robert K. Selander was helpful with advice on the study of molt, and, with Lois C. Stone, advised me in the preparation of the figures. Frances M. Weesner advised me in matters of histologic technique. Reggie V. Rausch prepared some of the histologic sections. Loye H. Miller kindly furnished information on the Anna Hummingbird. I am grateful to Robert T. Orr and G. S. Myers for making available specimens in collections under their care. Members of the staff at the University of California Botanical Garden aided in the work in that area, and among these I am especially indebted to Robert D. Dutton. Finally, I would like to thank Ward C. Russell and Jerry C. Russell for collecting critical specimens and Martha J. Williamson for assistance in preparation of the manuscript.

## MATERIAL AND METHODS

The data on territoriality and related behavior were obtained by field observation, from the spring of 1953 through the winter of 1954-55, in the Berkeley Hills on the east side of San Francisco Bay, California. Sixty-six specimens were collected in that area in the fall, winter, spring, and summer of 1954-55, for the study of the molt and testis cycles. In addition, specimens in the Museum of Vertebrate Zoology, California Academy of Sciences, and Stanford Natural History Museum were examined in the study of molt.

Two areas were used for the study of territory. One, a summer and fall feeding area,

is situated in the University of California Botanical Garden on the west side of the Berkeley Hills. The second, a winter and spring breeding area, is located in Tilden Regional Park on the east side of the Berkeley Hills. Although these areas are separated by only a short distance, they differ considerably in features of physiography and vegetation.

#### THE ANNUAL CYCLE

The Anna Hummingbird is a permanent resident throughout most of its range. However, it varies in abundance and activities in any particular location in a given part of the year. This applies particularly to the breeding season as contrasted with the season of subsidence of territorial activity, molt, and movement to favorable feeding areas in the dry part of the year.

The winter and spring months, from December to June, form the period in which the males are in reproductive condition and are occupying breeding territories. In the Berkeley Hills, the birds are found at this time in areas of broken chaparral, very frequently mixed with broad-leaved woodland of open character. They may also be found in riparian situations with willows and mixed shrubs predominating. The territories established consist of two distinct elements: (1) the core area, or primary territory, and (2) the buffer zone, or secondary territory (Pitelka, 1951*b*:644). The core area forms the center of activity of the male and contains one or more perches, usually on high stems, from which the male can observe in any direction about him. The majority of the songs, frequent chases, and all display flights originate at these perches. Chases of other birds, usually other hummingbirds, extend out over the buffer zone and often well beyond its boundaries out of view. Chatter and song usually accompany these flights as well as the more or less circular announcement flights made over the buffer zone. The breeding display and the dive display were rarely seen outside the core area.

The core area averages approximately one-fourth acre in size and occasionally is twice as large. The buffer zone varies in size and its limits are not easily defined. Pitelka (1951*b*:644), whose terminology of these areas is here adopted, estimated the size of the combined core area and buffer zone at six to ten acres.

Both of these areas are vigorously defended during the breeding season while the core area, or an area of similar size, is defended throughout the year. I have no records of one area being occupied continuously from one breeding season to the next, but such records are available (Pitelka, *loc. cit.*).

A male is usually promptly replaced when a territory is vacated, in some instances by a neighboring male and in others by a male not known earlier to have been in the vicinity. Frequent encounters between neighboring males are commonplace and each male seems well aware of the location of nearby males. In fact, some of the previously mentioned circuitous announcement flights pass over neighboring territories, and chases accompanied with chatter result.

In general, the winter and early spring months are the time of the year when the males assume the most belligerent and hostile attitudes, defending a large area by means of frequent, prolonged chases, abundant song, and the display flights characteristic of this species.

In May and June the behavior of the males undergoes marked changes. Display flights become infrequent and eventually stop entirely in most of the males. Territorial activity consists primarily of short chases in and about the core area which itself declines in size at localities where large numbers of birds feed. Molt commences in the juvenal males in late May and in the adults in early June. Coincident with the decline of territorial behavior in adults and the inception of molt in both age groups there is extensive movement, from the dry brushy hillsides, to areas of favorable food supply

such as gardens and other places where suitable plants such as tree tobacco and *Fuchsia* can be found. In these areas small territories are defended for varying periods of time by both adult and juvenal males, the former being more successful in this activity. In such places the density of birds may be great. By mid-August, defense of these small territories constitutes only a fraction of the activity seen in the breeding season. Song may be delivered quite regularly for considerable periods, but chases are brief and comparatively infrequent. Display flights are virtually absent and are performed by certain individuals only. At this time two males may frequently be seen feeding within a few feet of one another with no overt signs of hostility.

With the conclusion of molt in some adults in late August and early September, chases become more frequent and tend to be longer. By late September and early October many birds have finished molting and appreciable development of the testes has taken place. The tempo of territorial activity shows little further change until late November and early December. At this time the majority of the males, both juveniles and adults, have completed the molt and the testes are coming into breeding condition. In this period the winter rains commence and, in the local areas where suitable food in the rainy season attracts hummingbirds in numbers, females become increasingly more conspicuous in the dense population of males. Display flights increase abruptly, typically after a major spell of rainy weather, and movement to a suitable breeding habitat begins. By mid-December some males are still in the last stages of molt but all are in breeding condition. By January all the males are well established on breeding territories.

The evidence for the information presented here, except where otherwise indicated, is from my own field observations. Various aspects of behavior are outlined and described in papers of Pitelka (1942 and 1951*b*) and Woods (1927 and *vide* Bent, 1940: 371-387), which the reader may consult for additional information.

#### THE MOLT CYCLE

One object of the study of molt was to ascertain the period in which it occurred and its relation to the testis cycle and to the events in the cycle of breeding behavior. As will be shown later, a detailed study of the sequence of feather replacement has enabled me to set up arbitrary molt stages representing intervals in the molt process, thereby making possible estimates of the time required for both postjuvenal and annual molts. In addition this detailed study has revealed certain interesting features in the replacement of remiges, rectrices, and the gorget of the male. The manner and timing of molt in these areas may be linked with certain changes in behavior, in particular the display activity of the males.

Molt of the females was also studied. Although other aspects of the annual cycle in the female were not investigated, the information on molt alone makes possible certain interpretations of behavior which would not otherwise be possible. The comparatively brief five-month period in which adult females are molting terminates in October. From that time on they arrive in increasing numbers in the territories of the males. As will be shown later, this early appearance of the females results in increased activity of the males and possibly influences recrudescence of the testis.

A survey of the literature has failed to reveal any detailed account of molt in members of the family Trochilidae. Wagner (1955) has reported on certain aspects of molt in several species and Aldrich (1956) has recently provided some data on molt in the Allen Hummingbird (*Selasphorus sasin*). It is hoped that these observations in combination with the results reported here may form a basis for comparison among members of the family.

The data on period of molt and sequence of feather replacement have been derived

by examination of 421 study skins. Of the total examined, 165 specimens were actually taken while in the period of the molt, and these form the basis of most of the results obtained. Although no detailed study of pterylography of *Calypte anna* was undertaken, clipped alcoholic specimens were compared with other species described in the literature to enable me to apply the descriptive terms which have been used previously. The method of description is patterned after that of Pitelka (1945) for jays of the genus *Aphelocoma*.

*Pterylography.*—The pterylography of *C. anna* does not differ significantly from that reported for *Patagona gigas* (Thompson, 1901), "*Trochilus moschitus*" (= *Chrysolampis moschitus*) (Nitzsch, 1867), or *Selasphorus sasin* (Aldrich, 1956). The most thorough study of trochilid pterylography and the only one suitable for comparative purposes is that carried out by Aldrich (1956). All references to particular feather tracts and regions thereof follow his terminology.

A comparison of *Calypte anna* with *Selasphorus sasin* reveals the following differences in pterylography. Aldrich describes a vestigial seventh secondary for *sasin* which is not apparent in *anna*. Moreover, he indicates a number of greater secondary coverts larger than the number of secondaries, and this is puzzling. *C. anna* has six secondaries and six upper greater secondary coverts. The iridescent red feathers of the throat extend onto the crown in *anna*, covering the entire frontal region of the capital tract, whereas in *sasin* these specialized feathers are confined to the throat area.

*Age determination.*—It was necessary at the outset to segregate juveniles from adults. In males there are conspicuous differences that make such segregation easy. In females the differences are not so marked and in a few instances it was impossible to determine the age of the birds accurately.

The juvenal male differs most markedly from the adult in the coloration of the head and in the form of the tail. Young have a varying number of the red feathers on the crown and throat, usually only a scattered few, and never the complete complement of the adult. Interspersed among these are feathers of greenish-brown color, a few of these nearly always persisting until the last stages of molt.

The tail is useful for age determination in the early stages of molt. In the juvenal male, it is similar to the tail of the female in being composed of broad feathers with three distinct color zones: a green or grayish-brown inner zone, a black middle zone, and a white tip on the outer two and sometimes the outer three or four pairs of rectrices. The female has more white; the tips are broader and the white zone occurs on more feathers. The rectrices of the adult male are bluish-black centrally and grayish-brown laterally with the inner two pairs primarily green. Furthermore, the rectrices of adults are more narrow and attenuate in form, the outer pair strikingly so. Inasmuch as the tail feathers are replaced before the completion of molt on other parts of the body, the tail is not useful as an age criterion in the final stages of molt. The tails of an adult male, an adult female, and a juvenal male are shown in figure 1.

The only reliable difference noted that could be used to segregate juvenal from adult females was the form of the secondaries. This is shown in figure 2. In juveniles, both male and female, these feathers are rounded distally whereas those of the adult are truncate, or are pointed centrally, being incised slightly on either side of the rachis to form a shallow "W." At least one or two secondaries are among the last feathers to be replaced, and therefore juvenal birds can be distinguished in late stages of molt. There is some overlap in the variation of this character in the two age groups primarily as a result of wear; and as mentioned earlier, no precise age determination could be made for some females.

There is a fairly constant difference between the juvenal and adult females in the

number of red feathers in the throat region, although this is not completely reliable as an age criterion. The adults generally have a substantial patch of these feathers present whereas the juvenal birds have few or, more commonly, none at all. Adults sometimes have only a few, however, and so they cannot be distinguished on this basis alone.

No differences were detected in females in the form or coloration of the rectrices.

*Postjuvenal molt of the male.*—There were 78 specimens in juvenal plumage available for examination, and 72 of these were found to be in some stage of molt. The speci-

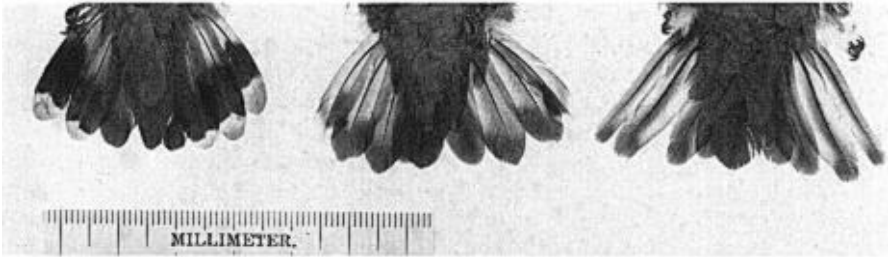


Fig. 1. Dorsal view of tails of adult female (left), juvenal male (center), and adult male (right) of Anna Hummingbird.

mens cover the entire period of molt and come from various localities in California, from Imperial, Los Angeles, and San Bernardino counties in the south to Sierra and Marin counties in the north. One specimen was taken in Pima County, Arizona.

Seven arbitrary stages of molt were defined after examination of the specimens (table 1). The sequence of feather replacement is consistent, and although some individual variation occurs in certain details in all areas examined, the general spread of molt over the body is orderly. The molt stages are plotted against time in figure 3.

No geographic variation in molt was found. Molt may begin as early as late May, and birds in the earliest stage of molt may be found as late as September. Molt in some birds continues into January and as some of these birds are in a middle or late-middle stage of molt, feather replacement undoubtedly continues in some instances into February. Thus, on a population basis, molt occurs over a period of eight to nine months.

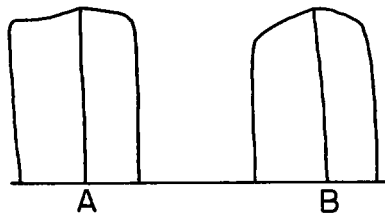


Fig. 2. Shape of outer secondaries in adult (A) and juvenal (B) Anna Hummingbirds.

That part of the period in which individual birds may be found in any stage of molt totals about four and one-half months. On the basis of the timing trend shown in figure 1, the postjuvenal molt in the individual is estimated to take approximately four and one-half months. In certain individuals there may be a retardation of molt in winter to the extent that it may require about six months. This view is supported by specimens in stage 5 collected as late as January.

The general sequence of the molt as well as its timing are summarized in table 1 and

figure 3. However, it is worthwhile to add to these condensed data remarks, first, on variation in the timing of molt over the body tracts and, second, on molt in the capital, alar and caudal tracts.

Spinal and ventral tracts. Molt begins in the sternal region of the ventral tract only slightly in advance of that in the anterior dorsal region of the spinal tract. Molt then progresses rapidly anteriorly and posteriorly in both of these tracts and spreads laterally more slowly. The ventral tract appears to be nearer completion at any given time, but both tracts may complete refeathering in the cervical region at approximately the same time.

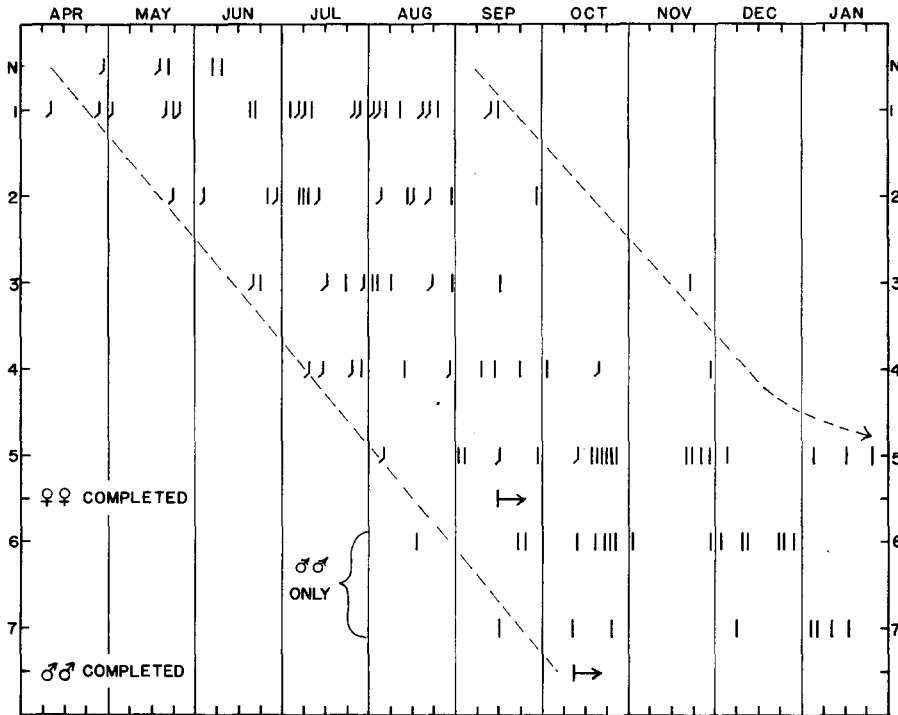


Fig. 3. Period of the postjuvinal molt in *Calypte anna*. Molt stages are described in table 1; N, no signs of molt; completion dates inferred from adults. Stages 6 and 7 apply only to males. Each female indicated by a hook at lower end of vertical line.

The interramal region of the ventral tract (gorget) does not undergo complete replacement until the molt elsewhere is complete or nearly so. At the time these feathers are dropped as a group, there may be a varying number of red gorget feathers already present. These specialized feathers evidently are replaced sporadically before and in all stages of the molt, and some recent ones may therefore be present when the overall molt of the face and throat occurs. These and the juvenal feathers of the region are replaced at one time. In a young male, one-third to three-quarters of the gorget may consist of red feathers at the time complete molt begins in the interramal region. Molt in this region coincides with molt in the loreal, malar, and frontal regions of the capital tract as discussed below.

Capital tract. Molt begins in the coronal and occipital regions at apparently the same time and generally commences shortly after inception of molt on the body tracts. The replacement of the post-ocular feathers that form the greenish-gray line between the red of the crown and gorget is variable in timing, but occurs in the course of the refeathering of the coronal and occipital regions. The frontal, malar, and loreal regions undergo complete replacement as a unit with the molt proceeding anteriorly. As with the gorget, a varying number of red feathers may be present at the time complete molt of

Table 1  
Arbitrary Stages of the Postjuvenile Molt

Stage	1	2	3	4	5	6	7
Ventral tract	Feathers of sternal region breaking sheaths; scattered or no feathers ensheathed on cervical, axillar and abdominal regions.	Scattered to many feathers breaking sheaths.	Scattered to many feathers breaking sheaths.	Scattered feathers still breaking sheaths; $\frac{3}{4}$ replaced to molt complete.	Scattered feathers basally ensheathed in cervical region; in few birds, interramal region may be covered with pin feathers.	Growth complete except for interramal region.	Extensive molt in interramal region.
Spinal tract	Scattered or no feathers breaking sheaths in the anterior dorsal region.	Feathers breaking sheaths.	Feathers breaking sheaths in the cervical and posterior dorsal regions or cervical and anterior dorsal regions.	Scattered feathers breaking sheaths in dorsal and cervical regions; $\frac{2}{3}$ replaced to molt complete.	Typically complete; scattered feathers may still be ensheathed in the cervical and posterior dorsal region.	Growth complete.	
Capital tract, dorsally	Scattered or no feathers breaking sheaths in the coronal and occipital regions.	Feathers of coronal and occipital regions breaking sheaths.	Feathers of coronal and occipital regions breaking sheaths.	Scattered feathers breaking sheaths in coronal and occipital regions; $\frac{1}{2}$ replaced to molt complete.	Typically complete in coronal and occipital regions; in few birds, frontal area may be covered with pin feathers.	Growth complete except for frontal region.	Extensive molt in the frontal region.
Capital tract, laterally		Some feathers of postocular region may be breaking sheaths.	Feathers of postocular region breaking sheaths, or still old.	Molt complete, or scattered feathers of postocular region breaking sheaths.	Postocular region complete; in few birds the malar region may be covered with pin feathers.	Growth complete except for loreal and malar regions.	Extensive molt in the malar region.

Table 1 (continued)

Stage	1	2	3	4	5	6	7
Primaries		1-4, 1-3, or 1-2 breaking sheaths; others old.	1-3, 1-4, or 1-5 fully grown; 6, 7, or 8-10 old.	1-6 fully grown; 7 breaking sheath to $\frac{3}{4}$ grown; 8-10 old.	1-8 fully grown, 9-10 old or incompletely grown.	Growth complete.	
Upper greater secondary coverts			Typically old; in birds molting secondaries they grade distally to proximally from ensheathed to $\frac{1}{2}$ grown.	Typically molt complete; may still be breaking sheaths or old.	Growth complete.		
Secondaries			Typically old; molt may start when primary 6 is dropped; secondaries 1 or 6 or both breaking sheaths, 2-5 old.	1 and 6 new or in various growth stages; 2-5 old.	Variable; 2 to 4 secondaries new, others incompletely grown.	Typically complete; up to 4 old secondaries may still be present.	Growth complete.
Upper tail coverts		Typically old, 1-1 may be breaking sheaths.	Typically new; 1-3 $\frac{1}{2}$ grown; 4-5 $\frac{1}{4}$ grown; or 1-1 pin feathers; others old.	Typically complete; may still be growing laterally.	Growth complete.		
Rectrices			Typically old; 1-1 or 1-1 and 2-2 breaking sheaths, or both pairs well grown.	1-1 and 2-2 dropped or incompletely grown; others dropped or old.	Typically pairs 1 and 2 fully grown, others old or breaking sheaths; or tail completely new.	Typically complete. Few birds have replaced 2 central pairs only.	



these areas commences. This phenomenon was noted by Woods (*vide* Bent, 1940:376), although the dates mentioned are misleading and no details are given.

**Alar tract.** The first feathers dropped are primaries 1-2, 1-2-3, or 1-2-3-4. The primaries molt in order until number 8 is replaced, and then primary 10 is dropped. This primary is always at least one-fourth and sometimes three-fourths grown, before primary 9 is dropped. Hence primary 9 is the last to be replaced. Primaries 9 and 10 are longer and more slender than the others in the series and undoubtedly are highly important in aerial maneuverability. Primaries 1 through 8 are always fully grown when primary 10 is dropped, giving the bird full use of the broad portion of the wing. Sequence of replacement of these two feathers is evidently related to the proper functioning of the outer margin of the wing, any impairment of which in the course of the molt is probably reduced by the precedence of 8 and 10, over 9.

The secondaries begin molt about the time primary 6 is dropped.

The greater primary and under primary coverts are replaced with the primaries.

When the first new primary or primaries are breaking sheaths, the marginal coverts begin replacement at the proximal side of the patagium. These coverts are completely new about the time primary 6 or 7 is fully grown.

The replacement sequence in the middle primary coverts is variable but always commences about the same time as that of the marginal coverts. The middle primary coverts may be dropped as a group or may be replaced more or less with the primaries, in both instances grading in development proximally to distally. The greater secondary coverts may begin molt with the primaries or may not begin until the primaries are one-half new. Molt of the secondary coverts precedes molt of the secondaries and they are usually fully grown when the secondaries begin molt. Exceptions occur, with one or two secondaries (1 and 6) being more or less ahead of the average growth stage among the coverts. I was able to discern that at least three out of nine birds commencing molt of the secondary coverts had secondary 1 or 6 or both well grown.

**Caudal tract.** Molt of the tail coverts begins when molt of the body tracts has proceeded posteriorly to the caudal area. These feathers drop as a unit and development of the incoming feathers proceeds most rapidly centrally. The replacement of the rectrices generally begins when primaries 1 to 6 are fully grown. At this time the tail coverts have completed development or may still be basally ensheathed. Although molt of the rectrices proceeds as in many passerines, from the central pair laterally, in this hummingbird some juveniles retain three or four lateral pairs of rectrices after the wing molt is complete. These may be retained for some time but they are always replaced before molt of the anterior portions of the head. The tail is replaced as two units with the two central pairs of feathers well grown or complete before the outer three pairs undergo replacement.

*Postjuvinal molt of the female.*—Forty specimens from various localities in California were available for examination, and of these 34 were taken in the period of molt. The arbitrary stages defined for the postjuvinal molt of males are applicable to the same molt of females. The early stages of molt in females involve additional loci, but these do not alter the timing of the molt. Stages 6 and 7, involving in the males molt of the red areas of the head, do not occur in the females. There are, in a few birds only, some deviations in the sequence of feather replacement not discovered in the males. These, however, are too slight and infrequent to justify establishing different criteria of molt progression in young females.

Molt may begin as early as the second week in April and birds in the earliest stage of molt may be found as late as the second week in September. The postjuvinal molt in individual birds is estimated to take approximately four months (fig. 3). Birds beginning to molt in September therefore do not conclude their molt until January.

Molt in juvinal females, then, occurs over a period about as lengthy as that for the juvinal males. However, from the plotting of the two groups in figure 3, it can be seen that there is a definite suggestion that postjuvinal molt begins and ends earlier in females than in males. This can be attributed in part only to the omission, in females, of stages 6 and 7; by reference to earlier stages it can be seen that as a group females are generally ahead of males.

In both males and females, the molt typically begins in the sternal region of the ventral tract. In the female, however, molt of this area is followed abruptly by the inception of molt in the interramal, coronal, anterior dorsal, and frontal regions, in the order given. In the male, as discussed earlier, there is no molt in the frontal and interramal regions until the last stages of molt are reached.

In addition, in the female, molt of the anterior dorsal region precedes somewhat any molt in the capital tract. The head of the female then undergoes complete feather replacement at the same time as the body tracts. In other respects the molt does not differ from that of the males.

I was unable to ascertain when the red feathers of the interramal region of the ventral tract are acquired. They do not appear in the months preceding the postjuvinal molt or are they acquired at the time of that molt. Virtually all adult females have at least a scattering of these feathers, which must therefore be acquired sporadically after the postjuvinal molt.

Two specimens were examined in which primaries 1 and 2 were fully grown, primary 3 was near completion, and molt in other areas had not commenced. These birds were assigned to stage 3, although there is reason to believe the body molt would be slightly delayed. Such variation is then reflected later, when, in both males and females, some variation occurs as to the time at which molt is completed on the body; it may be completed before or after molt on the alar and caudal tracts.

The postjuvinal molt of both sexes is complete.

*Annual molt of the male.*—Of 232 specimens examined, 45 were taken in some stage of the molt. Seven arbitrary stages of molt, defined after examination of the specimens, are summarized in table 2. No specimens were available that formed a second stage comparable to that described for the postjuvinal molt. This stage, involving a second activity in the primaries and inception of molt in the body tracts, is based on adult females. As with the postjuvinal molt, no geographic variation in timing or pattern of the annual molt was detected.

The general sequence of the molt and its timing are indicated in table 2 and figure 4, respectively. Molt may begin as early as the first week in June and, judging from the advanced condition of birds in later stages, even earlier. Refeathering of the head, the last stage in the molt, may occur as late as January. The period of time over which molt may be underway in at least some members of the population is eight months. The period of time estimated to be necessary for individual birds to complete the molt is two and one-half to three months. This estimate concerns molt exclusive of the red areas of the frontal, malar, loreal and interramal regions of the head. All molt, except that of the red areas, is completed before replacement on these begins. The interval, if any, I was unable to determine. Assuming that the interval is negligible, and with most of the gorget requiring no more than 10 to 15 days for replacement, the total period of molt in the individual is three to three and one-half months.

The second and subsequent complete molts of the male differ from the postjuvinal molt in the following ways: (1) Molt commences in the alar tract with the dropping of primaries 1 and 2. Only one specimen is available in this stage; however, specimens in later stages agree in that their remiges were evidently at least partly grown before molt on the body began. In the postjuvinal molt, on the other hand, the ventral tract was the first area on the body to begin refeathering. (2) In adults, molts in the spinal and ventral tracts closely parallel each other, and in some instances the spinal tract may be slightly nearer completion at a given time. This contrasts with the situation in juvenal males. (3) In the adults the replacement of the rectrices always commences when primaries

Table 2  
Arbitrary Stages of Complete Annual Molt

Stage	1	2	3	4	5	6	7
Ventral tract		Feathers breaking sheaths in sternal region.	Feathers breaking sheaths throughout tract.	Complete, or latest feathers breaking sheaths posteriorly and on neck.	Complete, or last new feathers breaking sheaths posteriorly and on neck.	Growth complete except interramal region.	Extensive replacement in the interramal region.
Spinal tract		Feathers breaking sheaths in anterior dorsal region.	Scattered feathers breaking sheaths throughout tract.	Complete, or latest feathers breaking sheaths in the posterior region.	Complete, or last new feathers breaking sheaths posteriorly.	Growth complete.	
Capital tract, dorsally		Feathers breaking sheaths in coronal regions.	Scattered feathers breaking sheaths in coronal and occipital regions.	Typically complete; scattered feathers may still be breaking sheaths.	Typically complete; scattered feathers may still be breaking sheaths.	Growth complete except frontal region.	Extensive replacement in the frontal region.
Capital tract, laterally		Feathers breaking sheaths in postocular region.	Scattered feathers breaking sheaths in postocular region.	Typically complete; scattered feathers may still be breaking sheaths.	Typically complete; scattered feathers may still be breaking sheaths.	Growth complete except malar and loreal regions.	Extensive replacement in the loreal and malar regions.
Primaries	1, 2 dropped.	1-2, 1-3 fully grown; 3, 4, 5 dropped, or 5-10 old.	1-5, or 1-6 fully grown.	1-7 fully grown, 8 dropped to nearly fully grown, 9 and 10 old.	1-8 fully grown, 9 old, dropped or growing, 10 dropped to fully grown.	Growth complete.	
Upper greater sec. coverts		Dropped.	Breaking sheaths.	Growth complete.			
Secondaries		Old.	1 dropped, old or breaking sheath, 2-5 old, 6 breaking sheath or fully grown.	1, or 1 and 2 fully grown; 3 old or breaking sheath; 4-5 old, 6 fully grown.	Variable. 1-2 or 1-3 and 6 fully grown; others old or incompletely grown.	Growth complete.	
Upper tail cov.		Old.	Breaking sheaths.	Growth complete.			
Rectrices		Old.	1-1, or 1-1 and 2-2 fully grown; others old.	1-1, 2-2 new, 3-3 old or breaking sheaths, 4-4, 5-5 old.	Pairs 1 and 2 fully grown; others in various conditions.	Growth complete.	

1-5 or 1-6 are fully grown. This timing may occur in the postjuvinal molt, or the replacement of rectrices may begin later.

Molt of rectrices in the adult usually begins with 1-1 and 2-2 emerging almost simultaneously, and the molt of the remaining rectrices usually proceeds rapidly. However, a slight interval is suggested between the first two pairs and the later ones, and it is of interest that the great delay that may occur in the young birds with the last three pairs of rectrices dropping near the end of the molt is reflected in the molt of the adult. Unlike the juveniles, there is no replacement of red feathers on the malar, loreal, frontal,

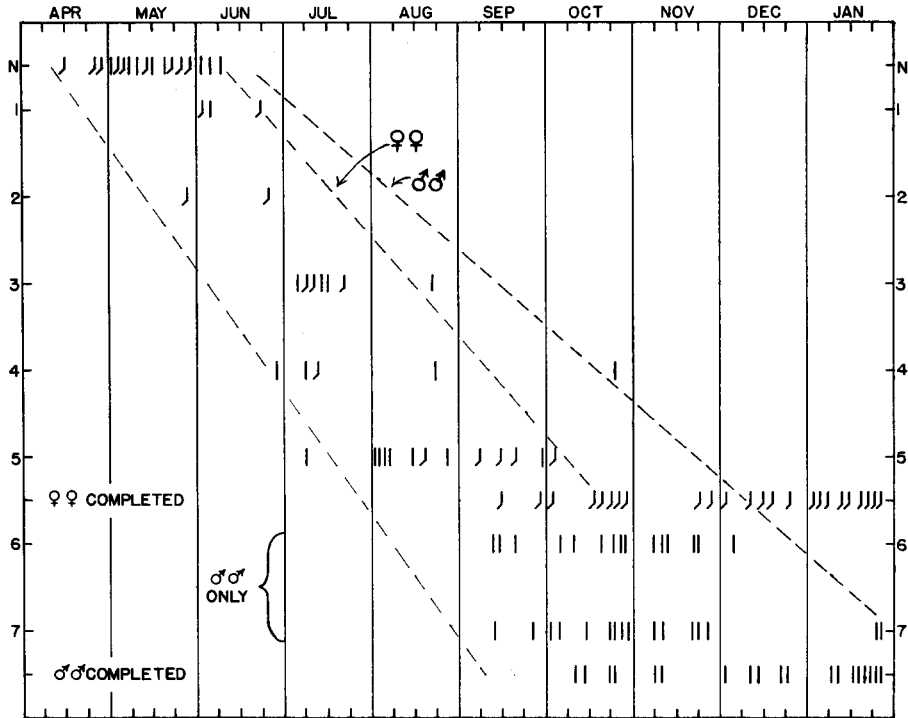


Fig. 4. Period of annual complete molt in *Calypte anna*. Molt stages are described in table 2; N, no signs of molt. Stages 6 and 7 apply only to males. Each female indicated by a hook at lower end of vertical line.

and interramal regions until molt on all portions of the body is complete. Adults proceed at this point to molt all the red feathers of the head, and this last stage is a very brief one. The head molt in adult and young males proceeds in similar fashion, that is, anteriorly. The sequence of feather replacement on the head is shown in figure 5. As previously indicated, the molt of adults lasts perhaps only three months as contrasted with the four and one-half months required for the postjuvinal molt.

*Annual molt of the female.*—Seventy specimens were examined, and of these only thirteen were taken in the period of the molt. The arbitrary stages defined for the annual molt of males are, with few qualifications, applicable to the molt of adult females. The early stages of molt involve the same additional loci on the head, discussed earlier for the juvenal females. Similarly, stages 6 and 7 do not occur. The only other variation noted is that from stage 3 on, usually in stage 5, some red gorget feathers are acquired

by the adult female, whereas in the immature ones, red feathers are apparently acquired after the regular molt. The dates for molt stages of the specimens are plotted with the adult males in figure 4.

Generalizations concerning period of the molt are difficult with such a small sample of specimens, but the molt apparently begins in early June and no birds in the earliest stage of molt were found after the third week in June. One specimen was in the final stage of molt in early October and several comparable ones were taken in September. It is estimated that molt in the individual birds may take two and one-half months for completion. The minimum period of time in which molt may be taking place in at least

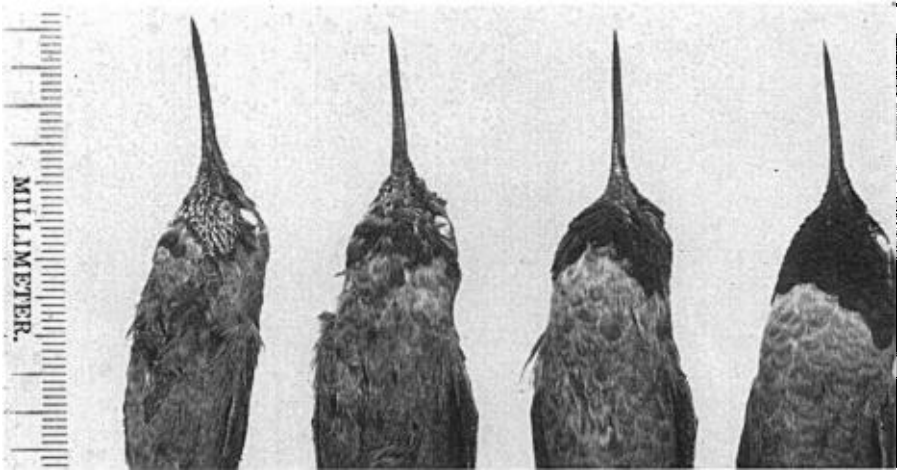


Fig. 5. Ventral view of heads of adult male Anna Hummingbirds arranged to show the sequence of feather replacement of the red gorget. Least advanced on the left; complete on the right. Note that molt proceeds anteriorly, the feathers at base of bill being replaced last.

some members of the population is five months. In light of the eight-month estimate for adult males it seems probable that this period is longer. As in the juvenal females there is an indication that the adult females may molt earlier as a group than the adult males.

As mentioned above, the annual molt of the adult female differs from that of males only in the molt of the head and in timing. In females this molt differs from the postjuvinal molt of the same sex only in the lack of activity in the interramal region late in the period.

*Discussion.*—The long period of nine months over which young of the year may be found in postjuvinal molt evidently reflects the long breeding season of the Anna Hummingbird. In one locality, Santa Barbara, this species may commence nesting activities in late December and continue until mid-June with two or possibly three broods per season (Pitelka, 1951a:198).

The time interval between fledging and the inception of postjuvinal molt is not known but this period appears to be lengthy. Young of the year are found in molt as early as mid-April and these may be presumed to be young from the first nestings. It is possible to estimate this interval more precisely by considering the late nestings and the birds most delayed in molt. If the presumed time necessary for postjuvinal molt, four and one-half months, is correct, and the last birds are fledged in June or early July, then at least two, and possibly three, months may elapse before molt begins. In addition.

retardation of the molt process may take place as evidenced by the following observations: (1) records of stage 5 in January; (2) the lengthy period sometimes necessary for full replacement of the body tracts; (3) the retention by some birds of several pairs of rectrices after most individuals have replaced these feathers; and (4) the fact that no birds were found in stage 1 later than September. Such retardation, whether it occurs on a significant scale or only occasionally, may be related to changes in food, qualitative or quantitative, in the course of the fall and early winter. It has been observed in the field that the birds congregate at this time about favorable food sources and the juvenal males are less successful than adults in maintaining feeding territories.

The molt of adults is similar in most respects to that of the juveniles. The molt of adults is briefer, being completed in three to three and one-half months in males and three months in females. It commences in the alar tract, whereas in the juveniles it commences in the ventral tract.

An estimate of 60 to 70 days for completion of molt in apparently several species is suggested by Wagner (1955:286). He did not attempt to separate sex and age groups, hence his results are difficult to evaluate. Further, Wagner reports for several species that molt begins in the alar tract, but again he fails to make a distinction between the postjuvenal molt and the annual molt of adults.

In males, over the anterior region of the head, parts of the capital and ventral tracts form the gorget and red crown, and these molt independently of the non-gorget portions of the same tracts. In females, on the other hand, there are additional loci on the head, and head feathers are replaced at the same time as body feathers. Some molt may occur in these regions in juvenal males before and in the course of the molt prior to the stage when the full complement of gorget feathers is acquired at or near the end of the molt. Wagner (1955:290) reports simultaneous replacement of iridescent feathers of the capital tract in *Eugenes fulvens*, but he does not mention whether this coincides with molt of the iridescent interramal region on the specimen he describes, as is true in *Calypte anna*. Further, he cites this as an "extreme" case rather than as a highly specialized mode of replacement, which is normal at least in *Calypte anna* and very likely in many other hummingbirds.

A strikingly different sequence of replacement of the contour feathers is discussed by Wagner (*loc. cit.*) for several species. He describes molt of the body tracts as beginning in the tail region toward the end of the molt of the rectrices and remiges. Replacement then proceeds anteriorly, terminating in the capital tract. I suspect that careful examination of a large series of specimens of any one of these species would reveal that this is not true.

The specialized head molt of the males is evidently related in timing to the onset of breeding occurring at the end of the molt period. The gorget, used in aggressive and breeding display, thus appears late in fresh, brilliant condition, and there appears to be a significant relation between completion of molt of this critical area and the consequent deferment of display behavior in any quantity until molt is completed.

There is a consistent irregularity in molt of the primaries in that the order of replacement is 1-8, 10, 9. This is apparently an adaptive device whereby aerial maneuverability is reduced to a minimum degree in the course of the molt. A somewhat similar phenomenon is noted in the molt of the tail with the central two pairs of feathers well grown or complete before molt of the outer three pairs commences. A similar sequence of primary replacement is reported by Wagner (1955:288) for *Calothorax lucifer*. In addition several modes of replacement for secondaries and rectrices are described by him for a number of species.

The inception of molt in the adults coincides with the close of the breeding season

in June when the days are nearing the longest of the year, and the dry season, with its associated scarcity of food, is well underway. The steady rise in mean monthly temperature and the decrease in amount of rainfall at this time of year are shown in figure 8. These, in combination with the changes in the light cycle, would seem to render very difficult, without experimental work, the discernment of the external factor, or factors, responsible for initiating the molt cycle. However, over the large geographic range occupied by this bird, the least variable climatic factor would seem to be the light cycle. Temperature and rainfall differ considerably from north to south in California. As mentioned earlier, it was recognized in the course of the study that the timing of molt inception and progression could not be linked with geographic location.

In June, also, the territorial behavior of the males is already undergoing marked changes through reduction in both the incidence of display flights and the size of the area defended (Pitelka, 1951*b*:645). There is a movement of large numbers of birds to areas of favorable food supply where small feeding territories are maintained for varying periods of time. Display flights are infrequent and performed by certain individuals only. Chases are short and relatively infrequent. The young males take part in this postbreeding dispersal and relocation but do not have the success of adults in maintaining feeding territories for any appreciable length of time.

Molt is generally completed prior to the onset of breeding activity in December and January when males were collected on breeding territories. The testes of both young and adults come into breeding condition in late November and early December although molt is still incomplete in some birds. Some adult males that are entering this period of breeding activity are still in one of the two last stages of molt and may remain so into January. In my records this is true of three out of 31. First-year males may be in any of the last four stages of molt at the beginning of the breeding season. This is true of 18 out of 49 records.

#### THE TESTIS CYCLE

It has been clearly indicated by earlier studies (Bent, 1940; Pitelka, 1942; Wagner, 1945; and others) that knowledge of the reproductive physiology of hummingbirds is a necessary prelude to an understanding of the complex territorial behavior of these birds.

An effort has been made to correlate certain events in the reproductive cycle with the climatic variables of day-length, temperature, and precipitation. In view of numerous attempts at such correlations for various passerine species, a comparison of some of these with the Anna Hummingbird seems desirable. Such a comparison is of interest in that this hummingbird is a north-temperate species breeding through the winter and spring, the males coming into breeding condition before the winter solstice.

As this study is primarily designed to develop correlations with behavior, emphasis is placed on the time relations of the reproductive cycle. No attempt has been made at detailed histological analysis. Specialized studies of the histology of the testis have been carried out for several species of passerine birds; a survey of this work is provided by Blanchard (1941) and by Blanchard and Erickson (1949).

The material for this study of the testis cycle consisted of 65 males collected from August, 1954, through September, 1955. The birds were skinned and the testes removed as promptly as possible following collection, usually within an hour. In some instances two to three hours elapsed before the gonads could be placed in a fixative. One bird was kept in a refrigerator overnight before the testes were removed. A comparison of histologic preparations from material fixed within 15 minutes and material not fixed for two to three hours revealed little difference. A similar comparison and finding is reported by Bullough (1942:167). The material was then treated in the following manner: fixa-

tion in Bouin's solution; dehydration in dioxane or alcohol; infiltration and embedding in paraffin; sectioning at  $7\mu$  and  $10\mu$ ; staining with Delafield's hematoxylin; counterstaining with eosin; and mounting in balsam. This is, in most essentials, the technique utilized by Blanchard and Erickson (1949) and renders the material adequate for comparison with a well-studied passerine bird.

Measurements were taken of the longest and shortest diameters of the larger of the two testes, usually the left. In most instances, the smaller testis of a pair was nearly equal in size to the larger one. Measurements were made with an ocular micrometer and calipers for the small and large testes, respectively. The volume of the larger testis

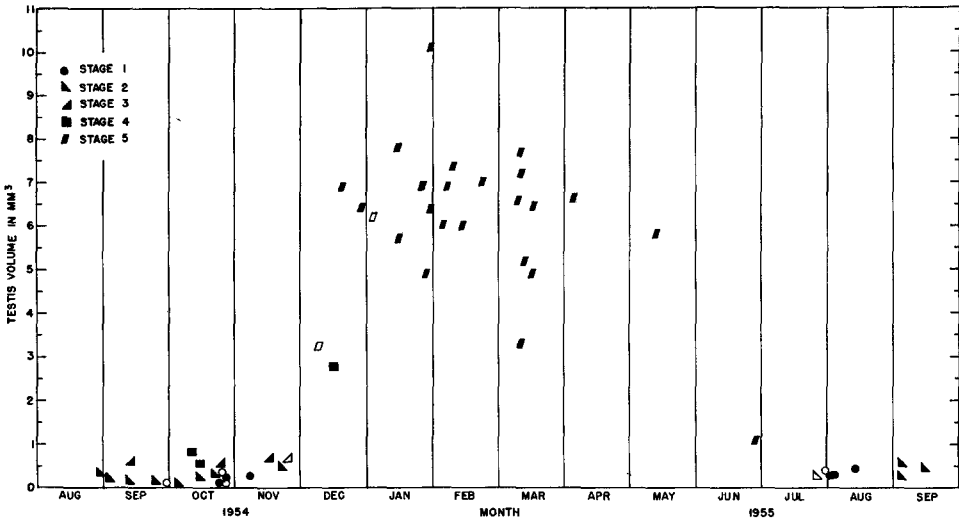


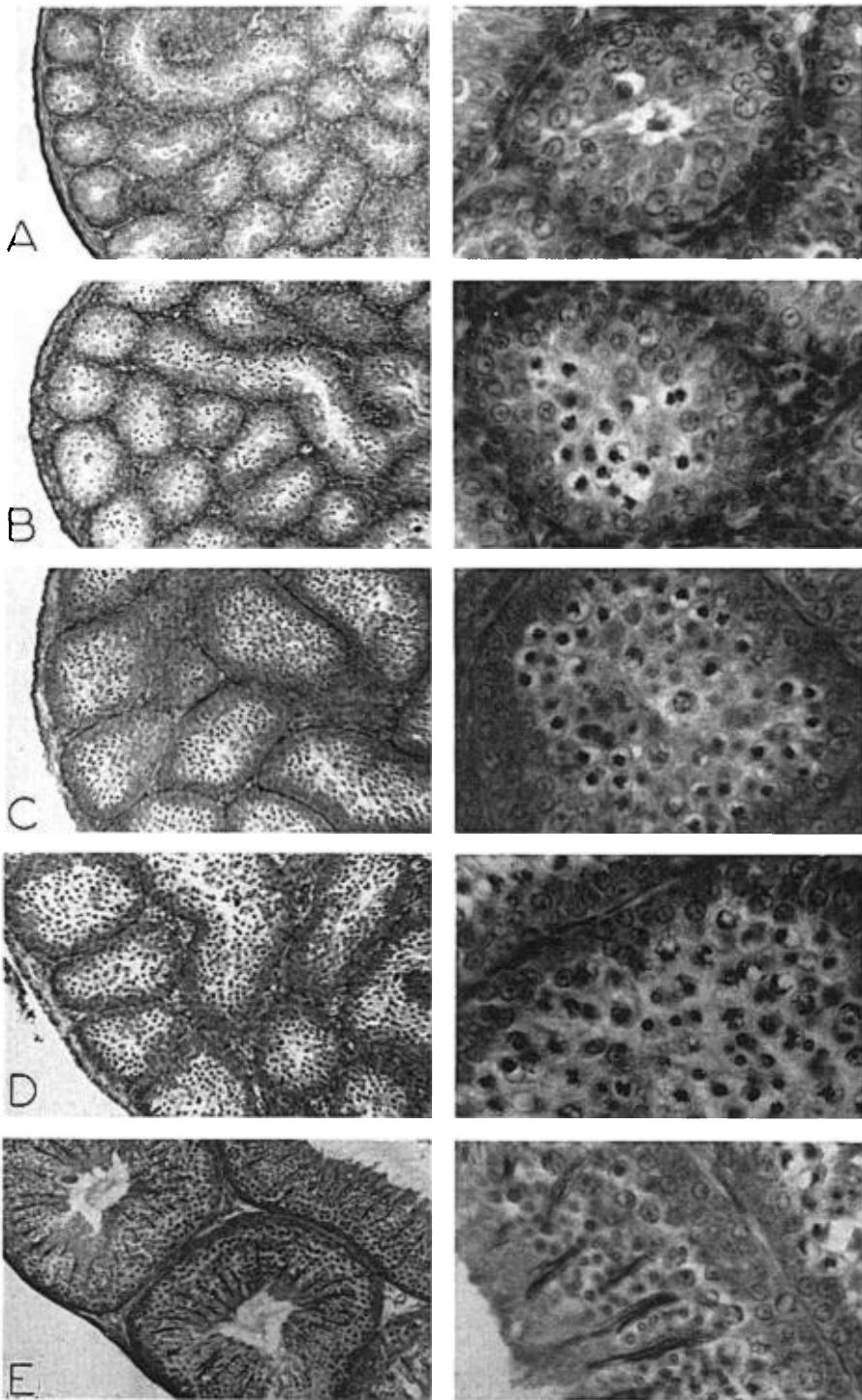
Fig. 6. The testis cycle in *Calypte anna* from August, 1954, through September, 1955. The solid and open symbols indicate adult and first-year birds, respectively. For definition of histologic stages see text.

was computed in cubic millimeters, using the formula for the volume of an ellipsoid,  $V = \frac{4}{3} \pi ab^2$ , where  $a = \frac{1}{2}$  the longest diameter and  $b = \frac{1}{2}$  the shortest diameter at the widest part of the testis. No weights were taken of any of the testes.

*Histologic stages.*—The histologic stages of the recrudescing testis in the Anna Hummingbird are, in most features, comparable to stages 3 to 7 described for the White-crowned Sparrow, *Zonotrichia leucophrys* (Blanchard, 1941). Stages 1 and 2 were not found and from the material available it is apparent that regression of the testes is not comparable to that in passerine birds inasmuch as no completely inactive state is reached. This might be suggested by the remarks of Wagner (1945:167-168) concerning the Mexican Violet-eared Hummingbird, *Colibri thalassinus*. Wagner states that some of the males of this species remain in the Valley of Mexico in the non-breeding season and that these birds "show all the exterior signs of readiness to breed, and the testes produce spermatozoa." Further he states that hummingbirds are capable of reproduction the greater part of the year except in the period of molt.

The testis stages and volumes are plotted against time in figure 6. The mean and extreme volumes for each histologic stage are shown in table 3. The juvenal males are included in both the table and the figure and in the discussion of the stages that follows.





The first-year males I collected showed no tendency whatever to be later than the adults in testis development.

A brief description of the histologic stages 1 to 5, approximately equivalent to stages 3 to 7 of Blanchard (1941), as they appear in *Calypte anna*, is as follows.

Stage 1 (fig. 7a). The tubules occupy the majority of the space within the testis and, although they are probably only slightly enlarged over the minimum size reached, each tubule contains two to four irregular rows of spermatogonia crowding toward the center. Many of these cells are dividing and a few appear to be degenerating. Primary spermatocytes are present in several of the tubules in

Table 3

Volume Mean and Extremes for Histologic Stages 1-5

Histologic stage	Volume range	Mean volume	Number of specimens
1	.06- .34	.24	11
2	.14- .63	.34	12
3	.48- .66	.56	4
4	.59-2.81	1.42	3
5	1.13-10.15	6.14	25

each cross-section and occasionally one is seen in synopsis. There is usually no apparent lumen and an area of clear cytoplasm fills the center of the tubule. Two to four rows of connective tissue cells are present encircling the tubules. Functional interstitial cells are abundant, filling the triangles or corners where three or more tubules meet and they are also present in irregular rows between the tubules. Scattered blood vessels are found in the interstitial area. The tunica albuginea is moderately thin and only slightly fibrous.

Stage 2 (fig. 7b). The tubules now have enlarged so that they almost completely fill the space within the testis. Five or six rows of spermatogonia occupy most of the space within a tubule. Nearly all the tubules in a cross-section contain a few primary spermatocytes in that stage of synopsis where the chromatin is on one side of the nucleus. A small lumen is present in some of the tubules. When present, the lumen is bordered by a narrow area of clear cytoplasm. The connective tissue cells are reduced to one or two rows between the tubules. The triangles between the tubules are filled with functional interstitial cells. Scattered blood vessels are present in the interstitial area. The tunica albuginea has become noticeably thinner and more fibrous.

Stage 3 (fig. 7c). The tubules have continued to enlarge and the intertubular spaces are now very restricted in size. Three to five irregular rows of spermatogonia now appear as a margin in the tubule with the remainder of the space occupied by one to five rows of primary spermatocytes in synopsis. Scattered secondary spermatocytes and possibly a few spermatids border the center of some of the tubules. The lumen is not so conspicuous as in stage 2, but it appears in some of the tubules. One or two rows of connective tissue cells can be seen between some of the tubules. The markedly reduced intertubular triangles contain functional interstitial cells. Blood vessels seem more conspicuous in the interstitial area, and the tunica albuginea appears the same as in stage 2.

Fig. 7. Histologic stages in testis cycle of *Calypte anna*; figures at left  $\times 125$ , at right  $\times 500$ .

A. Stage 1, increase in spermatogonia and presence of first primary spermatocytes. Immature male taken October 24, 1954; molt stage 6, slight fat.

B. Stage 2, primary spermatocytes in synopsis. Adult male taken September 26, 1954; molt stage 7, slight fat.

C. Stage 3, predominance of primary spermatocytes in synopsis, and first appearance of secondary spermatocytes. Adult male taken October 24, 1954; molt stage 7, slight fat.

D. Stage 4, first appearance of spermatids. Adult male taken October 14, 1954; molt complete, moderate fat.

E. Stage 5, breeding condition. Adult male taken January 13, 1955; molt complete, slight fat.

Stage 4 (fig. 7d). The tubules are very enlarged and now occupy virtually the entire area of a cross-section. Spermatogonia are present in one to three or four rows forming a margin around the rim of the tubule. Primary spermatocytes are arranged in three to four irregular rows, and the now more apparent lumen is bordered by several rows of secondary spermatocytes and spermatids. In one specimen some bundles of mature sperm are present, in groups of seven to twelve, their heads pointing outward from the lumen. Some connective tissue cells are still apparent between tubules and functional interstitial cells fill the intertubular triangles. Blood vessels are conspicuous throughout the interstitial area. The tunica albuginea is thin and fibrous, very similar to its appearance in stages 2 and 3.

Stage 5 (fig. 7e). The tubules are now of maximum dimensions and contain one or two rows of spermatogonia, one to three irregular rows of primary spermatocytes, and seven to ten irregular rows of secondary spermatocytes and spermatids. The latter completely encircle the large lumen and can be seen in various stages of metamorphosis. The lumina contain bundles of seven to 12 mature sperm arranged radially, their heads pointing away from the lumen. The lumina of most of the tubules contain free sperm, and in all there are accumulations of cytoplasm cast off from the metamorphosing spermatids. Connective tissue cells still are apparent between a few of the tubules and functional interstitial cells are at a minimum. The latter can be found only occasionally in the triangles or corners between the tubules. Blood vessels are conspicuous in the interstitial area. The tunica albuginea is extremely thin, and the nuclei are difficult to see and are very much flattened.

*Testis volume.*—The general picture of volumetric increase is shown in table 4. It can be readily seen that the greatest increase in volume takes place in late November and early December at which time the males are commencing display activities and moving onto breeding territories. Prior to this time there is no consistent trend in the population. Birds may be found with testes in any histologic stage from 1 to 4, at least in the months of October and November, and each of these stages has testis volumes averaging greater than the preceding stage. The broad overlap that exists in testis volume in histologic stages 2, 3, and 4 can be seen in table 3.

The picture that results shows certain deviations from that reported for the Starling, *Sturnus vulgaris* (Bissonnette, 1930; Bissonnette and Chapnick, 1930; Bullough, 1942) and the White-crowned Sparrow (Blanchard, 1941; Blanchard and Erickson, 1949). In these two passerine birds, testis volume in the population shows a gradual and uninterrupted increase up to the time that stage 6 (here stage 4) is reached. There is then a rapid increase in testis volume that slows down somewhat after breeding condition is reached. There is naturally some overlap in volume of particular histologic stages but not to the degree shown in the Anna Hummingbird. For example, Blanchard and Erickson (1949:270) indicate stages 1, 2 and 3 overlapping in volume; the same is true for 3 and 4, and 4 and 5.

Testis volume is not a criterion that can be used to indicate histologic stage in the greater part of the cycle (table 4). Testes of 4 mm.<sup>3</sup> or greater in volume may be assumed to be in breeding condition, but for those that are smaller no assumption can be made. The volume increases in stages 1 to 4, shown in table 3, are detectable only through computed averages for a number of specimens.

The range of testis volume in any given stage may be great, as indicated in table 3. Bullough (1942:174), working with the British Starling, attributed this, at least in stages 6 and 7 (here stages 4 and 5), to age. He assumed that the very old males have smaller testes. In the British Starling first-year males do not breed and consequently the testes do not reach the maximum size of the adults. In *Calypte anna* there is in addition great variation in the histologic condition achieved by various individuals of the same age at any given time prior to their coming into full breeding condition.

*Intertubular cells.*—As is apparent from the preceding section on histologic stages, I have recognized only three categories of intertubular structures: (1) connective tissue cells, (2) functional interstitial or Leydig cells, and (3) blood vessels. These are the

interstitial constituents recognized by Bullough (1942:176) and are the only ones discerned in the course of examination of my material.

The numbers of all these structures, with the exception of blood vessels, seem to diminish in abundance as the tubules increase in size. The most striking decline is in numbers of functional interstitial cells. In stage 5 these cells are difficult to find and appear only scattered in the triangles between the tubules. Whether or not these cells actually become less abundant, or only appear to do so because of increase in size of other portions of the testis, I am unable to say.

Table 4

Testis Volume and Histologic Stage for 15-day Periods, August, 1954–September, 1955

Dates	Volume MM <sup>3</sup> range	Average volume	Number of specimens	Histologic stages
Aug. 17–31	.35	.36	1	2
Sept. 1–15	.21–.66	.36	3	2–3
Sept. 16–30	.12–.18	.15	2	1–2
Oct. 1–15	.14–.86	.46	4	2–4
Oct. 16–30	.06–.48	.23	6	1–3
Oct. 31–Nov. 14	.21	.21	1	1
Nov. 15–29	.54–.59	.56	3	2–3
Nov. 30–Dec. 14	3.21	3.21	1	5
Dec. 15–29	2.81–6.93	5.40	3	4–5
Dec. 30–Jan. 13	6.23–7.85	7.04	2	5
Jan. 14–28	4.91–6.93	6.21	3	5
Jan. 29–Feb. 12	6.07–10.14	7.39	5	5
Feb. 13–27	6.00–7.09	6.54	2	5
Feb. 28–Mar. 14	3.39–7.76	5.91	5	5
Mar. 15–29	4.92–6.47	5.74	2	5
Mar. 30–Apr. 13	6.66	6.66	1	5
Apr. 14–28	.....	.....	.....	.....
Apr. 29–May 13	5.87	5.87	1	5
May 14–28	.....	.....	.....	.....
May 29–June 12	.....	.....	.....	.....
June 13–27	.....	.....	.....	.....
June 28–July 13	1.13	1.13	1	5
July 14–28	.....	.....	.....	.....
July 29–Aug. 13	.25–.42	.33	6	1–2
Aug. 14–28	.....	.....	.....	.....
Aug. 29–Sept. 12	0.34–0.63	0.48	2	2
Sept. 13–27	0.46	0.46	1	2

*Discussion.*—It can be seen in figure 6 and table 4 that there is considerable variability in the time at which any particular histologic stage is reached. This is especially interesting in view of the fact that all members of the population apparently come into breeding condition in a brief period of possibly two, and not more than three, weeks. In any event this was the situation in the fall of 1954 when this period covered the last week in November and the first two weeks in December.

In November, birds in histologic stages 1 to 3 were collected and birds in stage 4 were undoubtedly present as two in this stage were collected in October. Birds in stage 1 were collected as late as November 7, and birds in stages 2 and 3 as late as November 21. No additional specimens were collected until December 8, and from this date on, all those collected were in breeding condition with the exception of one male in late stage 4 collected on December 15.

The two males in stage 4 collected on October 10 and 14 indicate that some birds

can reach this advanced condition and remain so for an extended period of time. In passerine birds, stage 6 appears to be very brief with a prompt transition to breeding condition (Bullough, 1942:180; Blanchard, 1949:273).

It would seem, then, that a search for timing correlations between testis stages and environmental factors, which might be postulated to have an influence on the testis cycle, at least in the early stages of recrudescence, is of little purpose. There is an apparent lack of synchrony in the population in the autumn until that time when some factor, or set of factors, serves to bring the entire population into breeding condition at virtually the same time.

It was indicated in the section on molt that all the males collected were examined to determine the degree of feather replacement. This information was correlated with the stage of testis development and at least one interesting result is available. All the males in stage 4 had completed the molt and it would seem that the energy requirements of molt might have a direct effect on the rate of testis development. However, four other males that had completed feather replacement were in stages 1, 2, and 3. It may be, therefore, that completion of molt is a necessary prelude to early attainment of stage 4.

A system of classifying relative quantity of body fat was developed using the categories *heavy*, *moderate*, *slight* and *no* fat. Some of the birds were found to be completely encased in a jacket of fat but this apparently has no detectably consistent relation to either molt program or degree of testis development. Birds with slight, moderate, or heavy fat may be in any combination of molt and testis stages. The accumulation of fat deposits seems most likely connected with one of two possible sets of conditions: First, fat deposition may be linked with, and so preparatory for, the dry season of the year in late summer and early autumn and the paucity of food of that time. This shortage relates both to insects and nectar-bearing flowers, the primary foods. At this time of the year many individuals are molting, and the birds are moving about a great deal from one favorable locality to another. It would seem that the acquisition of fat at the onset of this critical period could be of distinct value in carrying the birds through the dry season. As indicated by Grinnell and Miller (1944:218), this situation has become less critical in recent years through the extensive planting of many non-native plants that flower abundantly in the period when native plants are quiescent.

The second possibility is that the birds are far less active from summer through the fall, and at least those fortunate enough to maintain feeding territories in favorable situations are more or less predisposed to becoming fat. This was true of all the males I collected in this interval. Activity was relatively scant and food was abundantly available in the particular area used as a source for my specimens.

It is apparent that the long reproductive period of the Anna Hummingbird, from December to June, covers the better part of the year, with the remaining interval occupied by molt. Even so, on a population basis at least, there is a varying degree of overlap of molt and reproductive activity both at the beginning and end of the breeding season.

#### CLIMATIC CORRELATIONS

The available data on histologic changes in the testes are not sufficient for any completely satisfactory correlations with annual climatic events. Only continued collection of material over a period of several years will produce results adequate for critical evaluation. However, some inferences as to the influence of climate on the breeding cycle can be deduced from my assembled data.

*Temperature.*—The monthly temperature data presented in graphic form in figure 8 can be easily contrasted with the data on testis development in figure 6. These give some indication of the relation of temperature to the recrudescing testes. It can be seen

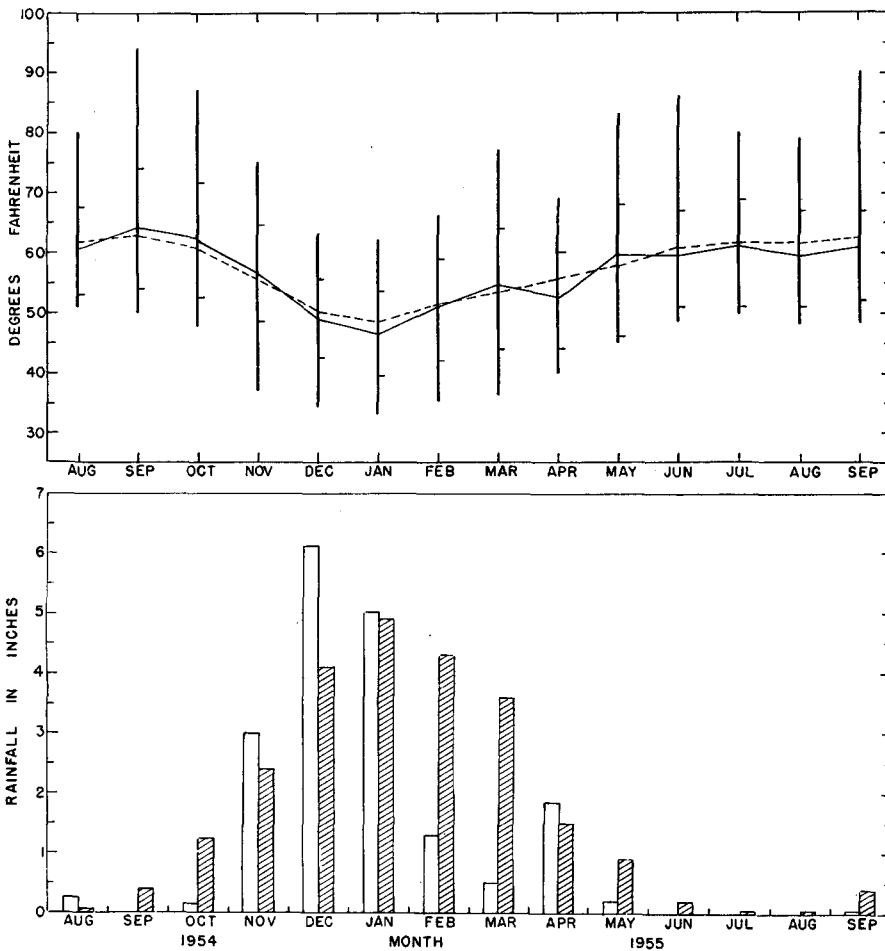


Fig. 8. Temperature and precipitation data for Berkeley from August, 1954, through September, 1955. Upper: Vertical lines represent temperature range (maxima, minima); horizontal lines indicate mean maxima and mean minima, for the month indicated. The continuous solid and dotted lines indicate mean monthly temperature during the study, and normal mean monthly temperature, respectively. Lower: Hollow and shaded columns indicate monthly rainfall during the study and normal monthly rainfall for Berkeley, respectively.

that recrudescence is in progress in the two warmest months, September and October, but that the greatly accelerated development of early December occurs while the temperature is declining. December, the first month when all the males collected were found in breeding condition, was only slightly warmer on the average than the coldest month of the year, January. The temperature then commences to rise and continues rising until the warmest month of the year, usually September.

Nesting commences in December and, for the population, probably reaches a peak in January and February (Pitelka, 1951b:648). These months are the coolest and generally the wettest of the year. This situation is evidently paralleled in some other species. For example, Skutch (*vide* Bent, 1940:452) makes some interesting comments concerning the nesting of the White-eared Hummingbird (*Hylocharis leucotis*) in very cool

weather in the highlands of western Guatemala. This species nests at or near the end of the rainy season, from October to December, when frequent frosts and cold winds prevail.

*Precipitation.*—The onset of heavy winter rains in November and December, shown in figure 8, seems to suggest a correlation with at least the terminal phase of recrudescence of the gonads. In the fall of 1954, the first substantial rains fell in the first 15 days of November with 1.47 inches recorded on November 15. There was an abrupt increase in territorial behavior following this initial heavy rain. No more precipitation was recorded until December, when rain fell nine out of the first ten days of the month. In this period, and shortly thereafter, the birds became established more or less promptly on suitable breeding territories and all males collected had mature sperm in the testes.

Again, Skutch (*vide* Bent, 1940:453) found that male White-eared Hummingbirds move to breeding territories and begin singing in the rainy season in August. The rain subsides in that area in October and flowering plants become more numerous. Breeding behavior then becomes more prominent. Cessation of breeding is coincident with the onset of the dry season in January. The cycle of breeding in *Calypte anna*, with regard to the rainy and dry seasons, is very similar. On the Pacific slope of southern Costa Rica, Skutch (*vide* Bent, 1940:435) found that several species of hummingbirds were breeding in the rainy season and early portion of the dry season when the nests of other birds were scarce. He also indicates that mountain inhabiting forms of hummingbirds in that area have breeding seasons that coincide with the rainy portion of the year.

*Day-length.*—Blanchard (1941:96–97) presents in graphic form the curve of variation in hours of daylight for Berkeley, and this can be referred to for particular information. It will suffice here to say that recrudescence of the testes begins sometime after the June solstice and continues, as the number of hours of daylight declines through the autumn. The birds come into breeding condition in late November and early December, before the winter solstice, when the days are approaching the shortest of the year.

*Discussion.*—The achievement of breeding condition seems more closely related to the onset of winter rains than to any other climatic factor. The number of consecutive days of rainfall appears to be of greater significance than the actual amount of rain received. Until further evidence is available it seems reasonable to assume that an inherent rhythm is operative in controlling the testis cycle, and that this rhythm is modifiable by rainfall and other factors, such as the presence of females, with the ensuing breeding season occurring in the period when food plants are most numerous.

It seems very probable that the presence of females has a modifying influence on testis development. I was able to detect a noticeable increase in activity of the males, including the performance of specialized displays, when females were present in the territories. Burger (1953:234), working with the Starling (*Sturnus vulgaris*), demonstrated that the presence of a female increases the magnitude of testis response by 45 per cent on given dates and under similar light conditions. Wagner (1945:171) believed the presence of female Violet-eared Hummingbirds caused increase in excitement among males.

Bené (1946:414–415), in discussing the Black-chinned Hummingbirds (*Archilochus alexandri*) is of the opinion that seasonal changes in light and temperature coincide with internal physiological rhythms regulating migration and initiating the breeding season. This is based only on the fact that migratory hummingbirds tend to reach the breeding areas in the period when flowering plants are available for food. This would not seem to be true of *Calypte anna*, or for that matter the many tropical, non-migratory forms.

#### SUMMARY AND CONCLUSIONS

An examination of the testis and molt cycles of the Anna Hummingbird has been coupled with year-long observations of territoriality and its associated behavior (fig. 9).

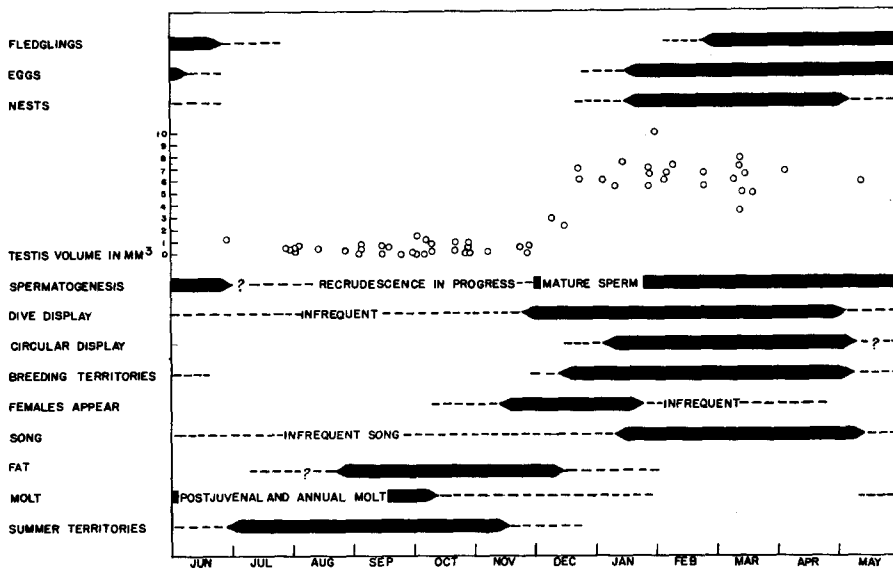


Fig. 9. Outline of general features of annual cycle of reproduction and behavior in the Anna Hummingbird. The solid bars indicate that the particular activity listed is in evidence; the dotted lines indicate a subsidence of the activity.

The molt of the males occupies a period from June to January, between breeding seasons. This process coincides with the dry season of the year and an associated paucity of food, at least in the normal or natural situation. During the molt males are relatively inactive, and many individuals become fat. The molt is modified to the extent that the feathers of certain areas critical in display and flight are replaced in a specialized manner at the end of the molt period. Molt in females is completed before that of males. Females then appear in increasing numbers in and about the territorial areas of the males, prior to the onset of breeding.

Recrudescence of the testes commences in the course of the molt period and is well underway in August. Testis development is not uniform in males. Some birds may reach the advanced condition of stage 4 while others are in various earlier stages of development. Regardless of this, all the members of the population come into breeding condition at approximately the same time, in early December. There is broad overlap of molt and the early stages of testis development, although molt is generally complete when the birds reach the breeding state. Recrudescence of the testes is probably influenced by a number of factors, including increase in winter rains and ultimate increase in food, the completion of molt, and possibly also the presence of females.

Territory size and defense vary according to the season of the year and the physiological condition of the males. During the dry season when the birds are molting, small areas are weakly defended. With an increase in testis volume, and a probable corresponding rise in hormone level, activity increases. When the breeding condition is attained, most of the males are established on large, actively defended territories.

The frequency and type of display undergo radical changes in the late fall as the breeding season approaches or begins. More complex displays appear and display in general is witnessed more consistently in that season. Many displays associated with defense of the small summer feeding areas are no longer seen.



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*Museum of Vertebrate Zoology, Berkeley, California, and Department of Health, Education, and Welfare, Arctic Health Research Center, Anchorage, Alaska, January 6, 1956.*