THE ANNUAL REPRODUCTIVE CYCLE OF THE CALIFORNIA GULL
I. CRITERIA OF AGE AND THE TESTIS CYCLE

By DAVID W. JOHNSTON

In the majority of avian species, and especially in small passerine birds, maturity is attained in the first year of life so that only two postjuvenal age groups are distinguishable, immature and adult. In many of the larger, non-passerine species, however, more than two postjuvenal groups have been described or suspected. This is true of gulls which undergo a protracted maturation period that sometimes involves three years. Prior to maturity, characteristic and distinctive plumages and molts can be correlated with specific ages, and certain recent studies of banded birds have corroborated the plumage sequences which had been indicated previously by the study of molting birds.

The present work deals specifically with California Gulls (*Larus californicus*) of known ages, identifiable on the basis of plumage and other characters, wherein special attention is devoted to annual conditions of reproductive anatomy and physiology in the subadult age groups as well as in adults. Previous investigations of reproduction in birds have in only a few instances been studies of complete annual cycles of both sexes, since the primary interest heretofore has been placed on male birds just before and during the breeding season. It is the purpose of this study to determine correlations among breeding activity, reproductive anatomy, migration, and age in both sexes, and to compare and contrast these data for the California Gull with previous investigations of annual reproductive activities in other birds.

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MATERIALS AND METHODS

Work was begun in August of 1951 and terminated in July of 1953. Until June, 1952, only sporadic observations were made and occasional birds collected, but, from June, 1952, to July, 1953, regular monthly observations and collections were made. During the fall, winter and early spring months, field work was carried out in the San Francisco Bay area of California where most of the gulls were collected at the garbage dumps of Oakland, Alameda, San Leandro, Berkeley, Albany and Richmond. During the late spring and summer months, most of the field work was done at Mono Lake, California, but some birds were obtained also from Honey Lake. Nonmigratory birds were collected in the San Francisco Bay area and at Clear Lake, California.

A total of 485 birds was taken over the two-year period, about 95 per cent of them in 1952–1953. A breakdown of this total according to sex and age is presented in table 1. The few specimens taken in 1951–1952 have been compared critically with birds of similar dates in 1952–1953 and in most instances have been included in the samples since no significant differences attributable to possible annual weather fluctuations were found between the birds collected in the two years.

Table 1

Numbers of Birds Collected from 1951 to 1953

	Males	Females
First-year	49	36
Second-year	48	52
Third-year	65	46
Adult	85	104
	247	238

A sample of five males and five females of each age group for each month was considered to be adequate for this investigation, although in some months this goal was not achieved primarily because sexual dimorphism is absent in this species. In the discussions of age criteria and various aspects of reproduction which follow, it will become apparent that, with relatively few exceptions, members of a sample of five show little variation in a given characteristic during the winter or nonbreeding months. Birds taken in the spring and summer, however, tend to be more variable, this being especially true of subadults as regards colors of soft parts and testis sizes. Even with these expected variations, it has been possible to indicate a normal or average condition for a characteristic according to age group and month.

DISTRIBUTION AND MIGRATION

The California Gull breeds on fresh-water or saline inland lakes of western North America from Great Slave Lake, Canada, south to Mono Lake, California, and from Klamath Lake, Oregon, east to Stump Lake, North Dakota. During the summer months, nonbreeding birds, principally subadults, occur casually along the Pacific coast from southeastern Alaska to Sonora, México. The winter range is almost exclusively the Pacific coast from British Columbia south to Oaxaca, México. Subadults are more plentiful than adults in the southern part of the winter range (Willett, 1938).

This species undergoes an east-west migration, at least in the fall. Birds banded as nestlings at Mono Lake, Klamath Lake, and Great Salt Lake have been recovered in winter along the Pacific coast with the preponderance of records being from San Francisco and Monterey bays, California (Woodbury and Knight, 1951).

Numerous observations indicate that in spring migration probably the bulk of the population moves into the Mono Lake area via the Owens Valley and that many of the migrants that utilize this route move on to other colonies farther to the north. Since there are recoveries in April of banded birds from Mono Lake in the San Francisco Bay area, and since there is a general tendency for this species to return to its natal grounds for breeding, it is also evident that a certain portion of the population reaches the Mono Lake area over the crest of the Sierra Nevada, thus carrying out a west-east migration in the spring.

After breeding, the gulls wander widely, especially throughout the montane lakes of the Sierra Nevada. For the fall migration there is additional evidence from observations and banding records that most of the Mono Lake population utilizes a transmontane route rather than the Owens Valley, although some birds probably use the latter route, too. Fourteen out of 17 recoveries of banded birds from Mono Lake in the late summer and early fall are from California localities north of Monterey Bay. This supports the idea that fall migration is essentially east-west and transmontane.

Field observations at local garbage dumps in the San Francisco Bay area indicate that, owing to competition with the larger species of gulls in winter, most of the California Gulls are absent from these favorite sites whereas they are common there in the late summer, fall, and spring. There is some evidence from banding records that some of these gulls move farther south: out of seven midwinter recoveries of birds which had been banded at Mono Lake, five are from scattered points around Los Angeles or farther south. Many of the gulls in the San Francisco Bay region, however, probably just move into adjacent habitats such as city parks and beaches.

In the early spring (March) a rather marked influx of California Gulls is noticeable at the garbage dumps whereas they had been absent, for the most part, during the winter. This increase might be attributed to one or more causes. Since it is coincident with the decline in numbers of the larger species of gulls, it is possible that the California Gulls are moving back to the dumps from the adjacent habitats just mentioned. It is also conceivable that there is an influx of birds which are migrating northward. The first of these two explanations is the more likely.

As further evidence that birds may migrate south from the San Francisco Bay area in winter and then return in the spring, it is possible to demonstrate a change in sex ratio from fall to winter to spring. If the birds collected at random in this area are enumerated according to sex and month of the year as in table 2, it can be seen that in the late summer and early fall there are almost equal numbers of males and females, but in midwinter more females are present. In March the ratio becomes balanced again. These data would suggest that either males migrate farther south or that they are absent from the dumps whereas the females are present. The first of these two hypotheses is favored, because if competition is a vital factor in keeping the species away from the dumps, it is certainly true that the males which are larger would be better competitors with the larger gulls than would the females. Differential migration of sexes has been demonstrated for other species of birds (Bullough, 1942; Mewaldt and Farner, 1953). There is also some evidence in table 2 that males migrate before females since in the first half of April relatively few males were collected. These samples are admittedly small, so the conclusions drawn therefrom must be tentative.

Table 2

Numbers of Males and Females Collected in the Nonbreeding Months

Month	Males	Females	Males : Females
August	14	14	1 : 1.0
September	19	21	1 : 1.1
October	24	27	1 : 1.1
November	18	19	1 : 1.1
December	12	29	1 : 2.4
January	10	20	1 : 2.0
February	9	21	1 : 2.3
March	18	15	1 : 0.8
April (first half)	7	14	1 : 2.0

DESCRIPTION OF THE MONO LAKE COLONY

For many years a large colony of California Gulls has bred on the islands of the highly saline Mono Lake. Dawson (1923) found the birds nesting on both Negit and Paoha islands and estimated about 850 nesting pairs on Paoha in 1919. The main colony, however, was located on Negit. In more recent years residents claim that the Paoha colony has been abandoned, perhaps due to the introduction of feral goats on the island, and, since at least 1938 when Nichols (1938) visited the lake, only Negit Island has been utilized.

The lake was visited on August 25, 1951, and in 1952 observations and collections were made from the shore at two-week intervals from May 16 to July 17. Between March 14 and July 20, 1953, five trips were made to the lake and Negit Island. A summary of the important events in breeding in 1952 and 1953 is presented in figure 1.

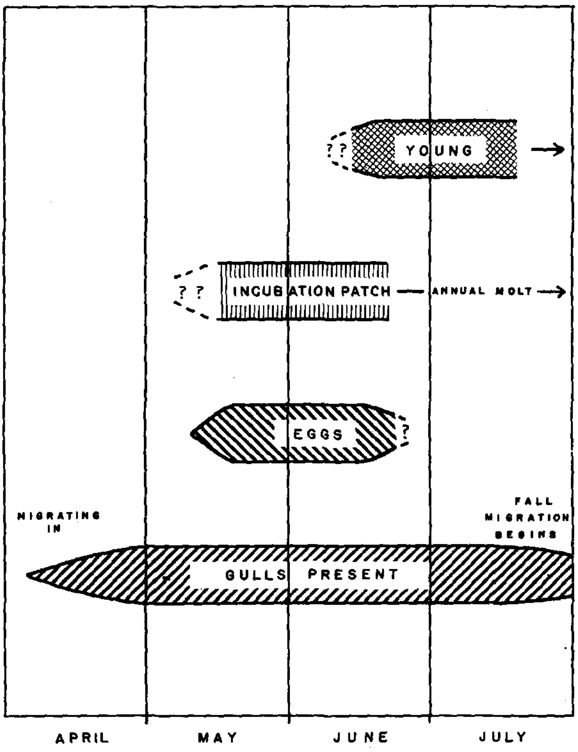

Fig. 1. Diagram of events of the breeding season at the Mono Lake colony in 1952 and 1953; question marks indicate suspected but unobserved conditions.

There were no gulls present on March 14, but by April 28 large numbers were present on and around the island. At this time there were no nests, and the birds lacked incubation patches. Most of the gulls had nests with eggs by May 15 at which time all adults collected had incubation patches. The nests were about six feet apart and were placed, for the most part, in the sandy pumice under the partial or complete shade of greasewood plants (*Sarcobatus vermiculatus*). Several eggs taken at random from nests contained embryos two to four days old, indicating that some eggs in the colony were laid about May 11. On May 29 and 30 embryos were, on the average, about two weeks old. In two different parts of the colony, 100 nests were tabulated, and the results are presented in table 3. These data, plus observations at other colonies (Honey Lake, California; Johnston and Foster, 1954:40; Pyramid Lake, Nevada, Marshall and Giles, 1953:113), show that the mean clutch size for this species is about two. On June 19 and

20 most of the eggs had hatched, some of the young being about one week old. Adults had incubation patches, most of which were beginning to refeather, this phenomenon marking the early stages of the annual molt.

Table 3

Summary of Two 100-Nest Censuses, May 30, 1953

Nest contents	East census	North census
One egg	16	12
Two eggs	66	54
Three eggs	17	34
Four eggs	1	0
Mean	2.0	2.2

From 3000 to more than 5000 gulls were estimated to be present at the Mono Lake colony, the range being partly a reflection of the difficulty in attempting to estimate flying gulls. Young (1952) has maintained that this colony is decreasing in numbers; he estimated that there were 1500 birds whereas Nichols estimated 3000 in 1938. Until a series of annual censuses is available, it is unwise to conclude on the basis of the existing sporadic and perhaps inaccurate records, the trend in numbers of this colony.

CRITERIA FOR DETERMINING AGE

It has proved necessary to re-examine the several criteria which have been used to determine age in the California Gull. In the past, various authors have utilized plumage and colors of soft parts, and to these I have added the length of the bursa of Fabricius, a dorsal evagination of the cloaca. By using these characters individually or collectively the age of a given bird may be determined as follows: first-year, 0 to 12–14 months of age; second-year, 12–14 to 24–26 months; third-year, 24–26 to 36–38 months; and adult, 36–38 months and older. The two-month interval is roughly an indication of the period of the annual molt at which time the bird is changing its distinctive plumage. Sexual dimorphism in the characters for determining age is absent, except perhaps in the bursa of Fabricius.

PLUMAGES AND MOLTS

Dwight (1925) considered the California Gull to be one of the gulls which has a four-year plumage cycle, that is, it molts into the adult plumage at the beginning of the fourth year of life. Following this generality he gave a detailed description (pp. 197–202) of the plumage and soft-part colors of each of the four ages, plus a limited amount of information on molts. Brooks (1943) disputed Dwight's interpretation, maintaining that the species undergoes only two complete molts and has only three plumage or age groups. He did not recognize the third-year plumage of Dwight.

Brooks' interpretation was erroneous because he considered a second-year bird (no. 1492, Comox, B. C., August 26, 1927) to be molting into an adult plumage. This specimen is molting, but, in view of the fact that new, smudged alulae are coming in and some of the new rectrices, which have not completely broken their sheaths, have dusky markings on the white background, this bird evidently is molting into the third-year plumage described by Dwight and summarized in a later section of this paper. Why Brooks denied the usual occurrence of this plumage is difficult to explain because there is a "typical" third-year bird in his collection (no. 8842, Okanagan, B.C., May 29, 1938) which is markedly different from the second-year bird in the same tray.

Poor (1946) in his study of plumage and soft-part variation in banded Herring Gulls (*Larus argentatus*) discussed this problem, stating that (p. 136) "Brooks (1943) disagrees with Dwight on the interpretation of the plumages of the California Gull (*Larus californicus*). Collected banded birds would resolve the conflict of these two authorities." This has been the approach undertaken by Behle and his students at Great Salt Lake, Utah. Birds banded as nestlings have been recovered in subsequent years at the breeding colonies, and the results of these investigations (Behle and Selander, 1953) have corroborated the findings of Dwight, both as regards plumages and colors of soft parts of the four age groups.

Despite this clarification, there is need for further analyses of molt. If four clear-cut plumage types can be recognized on the basis of banded material, it should be possible to establish this same sequence by utilizing a large sample of molting birds. An opportunity of this kind was afforded in the present study. Through the kindness of W. H. Behle, I was able to compare my unbanded specimens with representatives of each age group from the banded birds which are obtained at Great Salt Lake. In addition, four banded birds were taken by me, and these have been compared with banded and unbanded specimens.

In the discussion which follows only a general summary of the main plumage features is given supplemented by comments on deviations. Downy young and postnatal molt are not discussed. Beck (1942) gives an adequate description of these phases in the plumage cycle. Winter and nuptial plumages within a given age group are not separated because usually the two are rather similar. As will be pointed out later, however, such a separation is justified in some age groups because there is an extensive prenuptial molt of body feathers, more so than has been previously recognized.

Molt in relation to migration.—In all age groups, except for an occasional individual, the prenuptial molt is completed before the birds migrate. This statement must be made with some reservation because no birds were collected in early April at the breeding colony; it is possible that some of the earliest arrivals are still molting. On the other hand, the annual molt is rarely, if ever, completed before the birds leave the breeding colony. As figure 2 shows, all age groups are in their annual molt in June and July before they leave Mono Lake, and birds of all ages which have just returned to the San Francisco Bay area in August are still molting (except for the primaries and tail of first-year birds). Rectrices are apparently molted during and/or after migration; they were not found to be molting prior to migration.

Duration of molt.—It is significant to compare the present findings on duration of molt (fig. 2) with those given by Dwight (1925) and by Behle and Selander (1953). Undoubtedly, Dwight examined relatively few molting birds because he did not record second-year and adult birds as being in their annual molt in June and July, but, as can be seen in figure 2, this is the usual condition except for the rectrices. The prenuptial molt in this species involves primarily the body feathers, and from figure 2 it is apparent that this molt in third-year and adult birds occurs during February and March. Behle and Selander give the periods for the prenuptial molt as February to April for third-year birds and March and April for adults. A combination of their findings with those of the present paper would probably give a more accurate total picture of the duration of the prenuptial molt.

First-year.—By definition, this first-year category is intended to include three plumages described by the authors previously mentioned, namely, juvenal, first winter, and first nuptial. Except for the effects of fading and wear, and except for a few minor differences in seasonal appearances to be described later, I have found no obvious or consistent differences among these three plumages, and for this reason have combined them. This plumage type or age group spans a little more than a twelve-month period because it begins with the plumage assumed at the postnatal molt, acquired by the Mono Lake

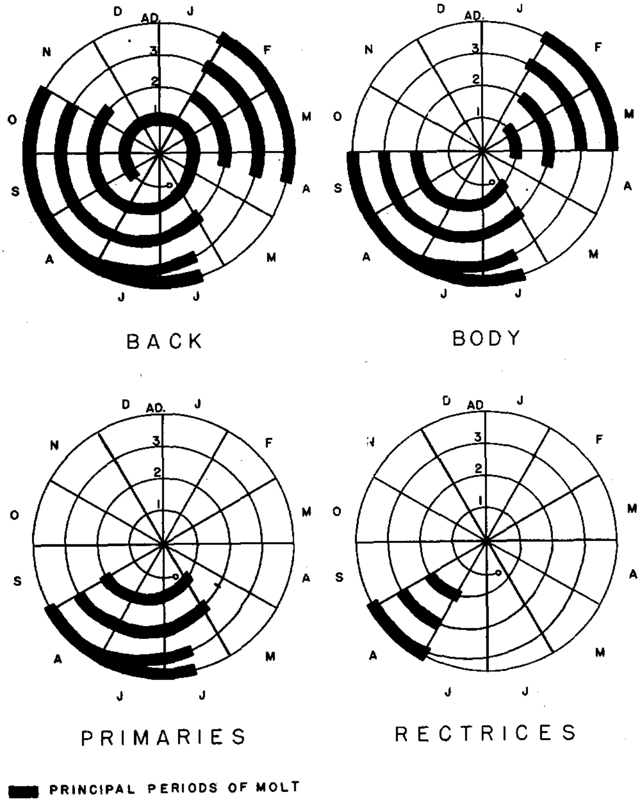

Fig. 2. Molt cycles in the California Gull. Body includes head, neck, breast, abdomen and flanks.

birds in late June and July (late May and June at Great Salt Lake). Birds during the first year are characterized by having blackish brown primaries, rectrices with broad and variable brown and white barring, and underparts, head and neck mottled with brown and white. As Behle and Selander indicate, the back or mantle changes from the brown and white pattern in the first fall and early winter to an admixture with pale blue-gray feathers in the first spring.

A banded female of this age group was taken on October 17, 1952, at Oakland, Alameda County, California. It was banded at Yellowstone Park, Wyoming, as a nestling on July 16, 1952. Its plumage was the same as that of unbanded birds generally considered to be in their first year and as that of another banded first-year bird taken by W. H. Behle at Great Salt Lake.

According to both of the major studies on plumages cited, a partial postjuvenal molt supposedly occurs from September into the winter. Apparently this is not true in most instances, at least as regards body feathers. In at least 46 birds examined between July 31 and January 1, relatively few showed any signs of over-all molting. As far as the body areas (explained in fig. 2) are concerned, no molt was found until October 29, and in the following two months it occurred in only 5 out of 20 birds. The winter, then, is not a time of principal molt of these feathers in this age group. The upper back, or "mantle," however, showed a rather continuous molt beginning in August and extending, in most birds, on into the spring. Thus, it would appear to be more accurate to speak of a first winter molt, involving, for the most part, only the feathers of the upper back until February when a rather extensive molt of the body, head and neck areas commences. During the spring months, these areas are still mottled with brown and white, although the over-all appearance is somewhat lighter than for young birds immediately after they leave the colony the previous year.

The first annual molt begins in most areas of the body before the annual molt in any of the other age groups. This is correlated with the fact that birds of this age group do not breed. As far as I was able to determine, the first annual molt is complete.

Second-year.—The first annual molt is a transition between the first-year and second-year plumages, and, largely for the sake of convenience, the second-year plumage is assumed to begin on the first of August, even though the molt might not be quite complete.

Again, I have combined the winter and nuptial plumages in this age group, and, except for a few body areas, this seems to be a logical procedure. The second-year plumage is characterized by gray-brown primaries as opposed to blackish brown in the first-year, by an occasional primary with a faint whitish mirror showing on the inner vane, by gray-black rectrices with a basal portion lighter and with less barring than in the first-year birds (see Dwight, *op. cit.*:355, fig. 112), and by a body generally mottled with gray brown but whiter than in first-year birds. The mantle is usually entirely blue gray, but there may be a scattering of gray-brown feathers. There is considerable variation in patterns of the secondary coverts. In most birds some or most of any row may be blue gray, but usually the greater secondary coverts are mottled with brown and white, somewhat similar to but with less broad areas of white than in the first-year birds. Gray secondary coverts are more frequent proximally. Also, the first four primaries may be either grayish white or gray brown like the distal ones.

One banded female was taken at Bay Farm Island, Alameda County, California, on March 4, 1953. It had been banded at Pyramid Lake, Nevada, on July 6, 1951, and was therefore in its second-year plumage. This bird was identical with unbanded birds of the same age group and with a banded representative from Great Salt Lake.

During the fall and early winter, birds in the second-year plumage continue to molt a few body and back feathers, but the back molt is not as continuous as it is in first-year birds. Prenuptial molt commences in January and continues until April during which time the new feathers of the body, head, and neck may be replaced with white or gray-brown tipped feathers. In April and May, these birds have white heads and necks mottled or streaked with dark markings, and their underparts may be completely white or partly gray brown.

Third-year.—This is undoubtedly the most variable plumage in the species. In general, third-year birds differ from second-year birds by having black and white-tipped and/or black and white-mirrored primaries, all white underparts and the black of the rectrices confined to a narrow terminal or subterminal band. It is necessary to know the variations in these areas and their combinations so that the age can be correctly determined.

In almost every bird, either the ninth or tenth primaries or both have a subterminal white mirror on one or both vanes. The first four primaries are entirely gray except for number 4 which may have a subterminal black band. At least the distal five or six primary coverts have blackish outer and somtimes blackish inner vanes. The four alular feathers almost always have distal blackish vanes, but occasionally one or more of these are gray. The secondaries are most commonly gray with blackish smudges distally on their outer vanes. Some or nearly all of these may be entirely gray. Secondary coverts are exceedingly variable, but usually almost all of them are gray as in adults. There may be an occasional gray-brown lesser covert which perhaps was not replaced from the second-year plumage. The median coverts are almost without exception all gray, but the greater coverts may be gray or brown and white-edged as in second-year birds. In the latter instance, these do not appear to represent feathers which did not molt from the second-year because they have a grayer appearance than similar feathers in the second-year birds.

The mantle is entirely gray and the underparts are white. In winter the head and neck have a streaked appearance.

Variation in the rectrices runs the gamut from a broad, subterminal or terminal black band to completely white in rare individuals (see Behle and Selander, *op. cit.*, plate 7). Sometimes only one or two feathers have a single black spot. The few individuals (four) that had a completely white tail were judged to be third-year on the basis of other plumage characters, colors of soft parts, and the length of the bursa of Fabricius.

Out of 111 specimens of this age group, I obtained only one which lacked blackish alulae. It had, however, most of its secondaries with black smudges, much black in the tail and the typical third-year soft-part colors of that season. Blackish alulae against the background of blue-gray secondary wing coverts, usually involving all four feathers, is one of the most constant characters of third-year birds.

The back and body areas show about the same duration and frequency of molt as in second-year birds. The prenuptial molt, involving back, body, head and neck feathers, lasts from the end of January until about the first of April and results in a head and neck which are sometimes entirely white, although usually a few dark streakings remain.

The third annual molt begins in the middle of June in contrast to the commencement of this molt in the younger age groups at the end of May. The difference is explained partly by the fact that some third-year males breed. Nonbreeders of this age group apparently do not molt any sooner than the few that breed.

Of particular importance has been the collection of several birds which were molting from the third-year into the adult plumage. One of these shows a new gray alular feather and three old blackish ones. Others show old third-year primaries with a small mirror that are being replaced by primaries with a large subterminal mirror and blackish-smudged secondaries that are being replaced by entirely gray secondaries.

Adult.—These birds have blue-gray backs, wing coverts and alulae, outer primaries with black distal portions and white tips, primaries 10 and usually 9 with a white subterminal mirror or long white tips involving one or both vanes, blue-gray secondaries with white tips, and all white tail, underparts, head and neck. In the fall and winter, the head and neck are streaked. In contrast to the variable third-year plumage, adults were found to be more uniformly alike in the 189 birds collected, but Behle and Selander collected at least 8 specimens the age of which was difficult to determine correctly. In the present study by using a combination of characteristics, it was possible to determine the age of all specimens. Some of these have already been discussed in connection with third-year birds. In order to show some of the exceptional variations in this age group, the few variable adults which were collected and their characters are given below; only the characters which deviate from the usual adult plumage are mentioned, these birds otherwise being like typical adults: (1) Four birds, each of which had one partly blackish alular feather. This is apparently an expected variation in adults because Behle and Selander obtained a banded adult with this feature. (2) One bird with three blackish alulars and five secondaries with small black smudges. (3) One bird with a small black spot on two rectrices. (4) A banded four-year-old female was taken on January 30, 1953, at Albany, Alameda County, California. It had been banded on June 4, 1949, at

Great Salt Lake and was therefore in an adult plumage. It has one partly blackish alular feather. Erroneously, I reported to Behle and Selander (*op. cit.*:256) that this bird had a white tail "with numerous pale dusky markings," but careful re-examination of these markings has revealed that they are adventitious stains. The primary coverts of this bird are not dusky, and the secondaries are blue-gray.

During the fall most of the adults show some molting back feathers, and even in November and December occasional birds were molting some of these feathers. From the end of January to about the middle of April, a prenuptial molt of these feathers was very noticeable. Somewhat similarly, molt of body feathers was found sparsely in some adults from the end of September until November, but it was mostly lacking during the winter until the end of January at the commencement of the prenuptial molt. The prenuptial molt, involving feathers of the back, head, neck, abdomen, breast and flanks, is more extensive and intensive in adults as compared with the other age groups, and it is as extensive and intensive as in the annual molt. Adults, at the culmination of the prenuptial molt, and prior to spring migration, have completely white heads and necks.

The annual molt is approximately the same as in third-year birds. This is as one would expect since third-year birds molt into the adult plumage at this time. Adults begin to molt soon after or as the eggs are hatched, and, as far as I was able to determine, males and females begin this molt at about the same time. Since both third-year and adult birds begin the annual molt later than the first- and second-year birds, it is instructive to note that Wynne-Edwards (1939) has found a comparable condition in the Fulmar (*Fulmarus glacialis*) in which species the nonbreeding immatures begin to molt sooner than adult breeding birds.

COLORS OF SOFT PARTS

One of the most useful sets of characters used in determining the age of gulls is the color of the soft parts. In the several major works (Dwight, Brooks, Behle and Selander) which have dealt with this in the California Gull, there have been considerable differences in the descriptions. The discrepancies have been due primarily to normal color variation within an age group (for variation in a single character in a given age, see Behle and Selander, *op. cit.*, table 3, p. 247). As in most of these previous works, color notes in the present study were taken under field conditions on a purely subjective basis without reference to any standard color key. With the possible exception of Dwight, other workers have not attempted to give a complete annual picture of these characters, and even Dwight was somewhat sketchy and generalized.

In none of the works cited or in the present study has any consistent sexual dimorphism been found in the colors of the soft parts. Therefore, in the discussion to follow, the data for the sexes are combined.

Bill.—A summary of seasonal variations in bill color for all age groups is presented in figure 3. These diagrams represent average conditions of coloration only, for color variation may occur between birds of the same sex and age taken on the same day. If one-half of the birds in a given age group during a given month had bill parts of one color and one-half another color, both of these colors are presented in the figure; for example, during April approximately one-half of the adults had an orange-red spot on the lower mandible, but an equal number had this spot vermilion.

Birds from recently hatched eggs on June 20, 1953, had bills entirely black except for the light pinkish tips and the egg tooth. As the birds grew to be juveniles, the basal portion began to lighten and the tip remained a creamy white (Behle and Selander, *op. cit.*:245). Soon after leaving the breeding colony in July, however, the original coloration was more or less reversed because at the end of July a bird-of-the-year had a bill

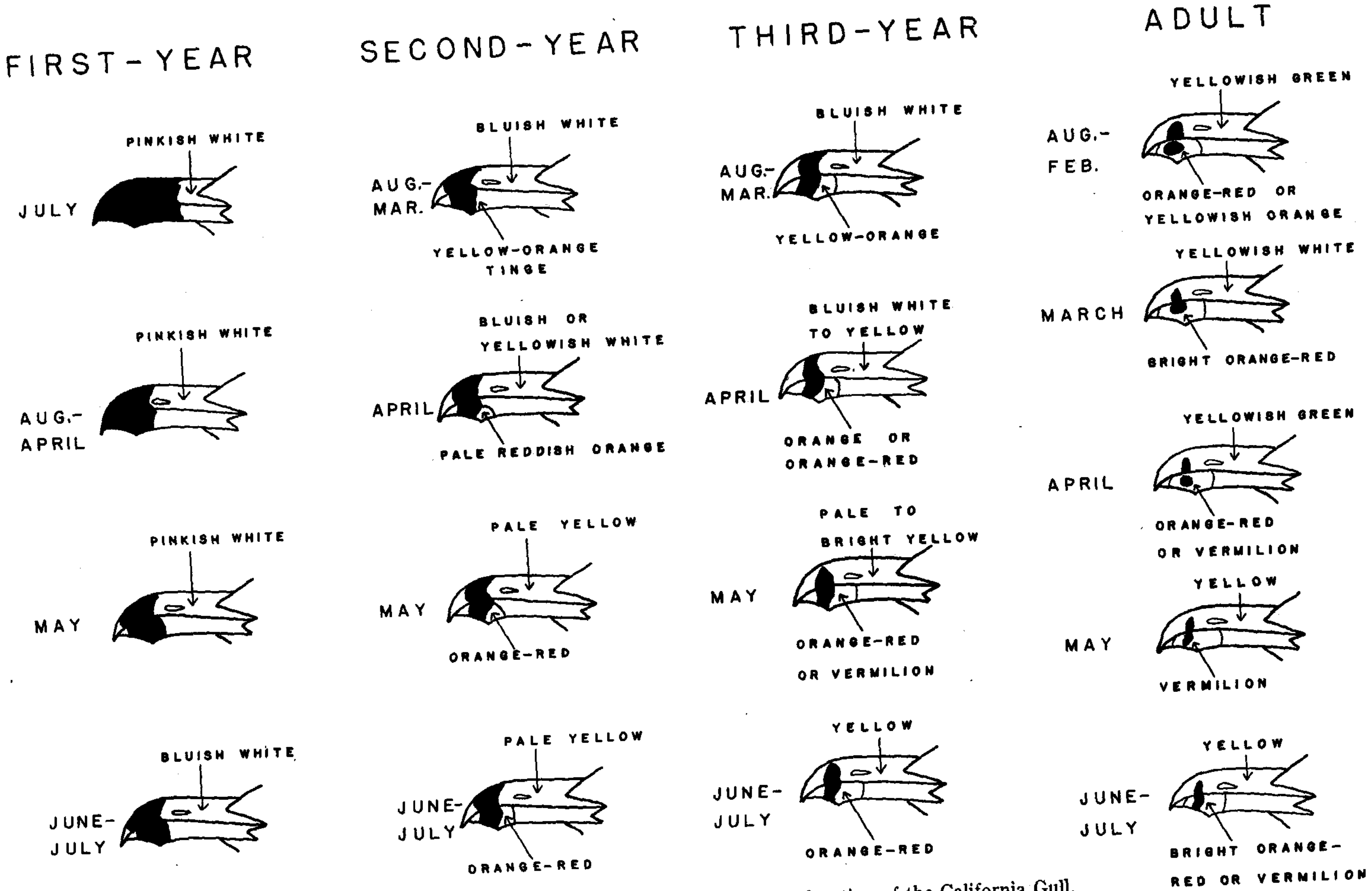

Fig. 3. Seasonal and age variation in bill coloration of the California Gull.

that was basally pinkish white, but more than one-half of the terminal portion was blackish. Changes subsequent to these initial colors are indicated in figure 3.

It has been conclusively demonstrated that bill coloration in some species of birds is under the control of male sex hormones. Significant among the studies conducted on androgenic control was that of Keck (1933) on the English Sparrow (*Passer domesticus*). He demonstrated that the bill of the male changed from horn brown or ivory in the nonbreeding season to black in the breeding season under the influence of male sex hormones. These results have been corroborated by Witschi and Woods (1936) in a more intensive investigation of the histological picture of melanophore dispersal and development. The change in bill color to black coincided with the development of the testes to a maximum breeding condition. Further work on feral English Sparrows by Davis (1953) has shown that at least some birds-of-the-year (3 out of about 100) in June and July not only had testes in breeding condition but also black bills, both characters the same as in breeding adults taken at the same time. In view of the experimental results of Keck and Witchi and Woods, it would seem that these few juveniles were producing enough androgens to evoke a change in the bill color.

In the British Starling, Bullough (1942, figs. 13–36, p. 197) has drawn and described seasonal changes in the bills of adult males and females. From about June through November, the bills of both sexes are predominantly dark gray, but they become progressively yellower in the breeding months, especially in February and March. Juveniles and first-year birds have dark bills until February at which time yellow color develops, again coincident with gonadal recrudescence. This change in color from gray to yellow was attributed to the production of the male hormone by the testis. Witchi and Miller (1938:468) have demonstrated that the bills of both sexes in captive birds turn yellow under the influence of androgens but do not react to estrogens.

In the Herring Gull (*Larus argentatus*), a close relative of the California Gull, there is further evidence (Boss, 1943) that bill coloration is under androgenic control. Poor (1946) reported on banded Herring Gulls in which colors of soft parts, in addition to other characters, were given for individuals of known ages. The matter of seasonal bill coloration was summarized for this species and is generally simliar to that in the California Gull. If this work of Poor on birds of known age and the work of Dwight (*op. cit.*: 180–197) based upon molting and nonmolting birds are considered as natural background, comparison may then be made with the results of hormonal investigations conducted by Boss. He injected testosterone, stilbestrol, thyroxin and gonadotropin into different groups of nestling birds. The testosterone-treated birds of both sexes matured in one year, but controls and birds injected with the other hormones required the full three years to acquire the mature plumage, behavior, and colors of soft parts. In experimentals the bill changed from all black to the adult type, yellow with a red spot. It would seem, then, that bill coloration is directly under androgenic control in both sexes.

Similarly, in the Black-headed Gull (*Larus ridibundus*) van Oordt and Junge (1933) have shown that the bill becomes crimson during the breeding season but is flesh-colored in the nonbreeding months. Castrated birds developed the crimson color when injected with male hormone.

In view of all these experimental results, particularly those on the closely related gulls, it seems safe to conclude that this character in the California Gull is also under androgenic control.

Leg.—Previous workers have indicated that the colors of legs and feet are the same, but experience with fresh California Gulls indicates that this is not always true. In many instances the color of the feet differs widely from the color of the tarsometatarsal region, which is somewhat variable in itself. In an attempt to reduce the numbers of variables, therefore, only the predominant color or colors of the tarsometatarsus were recorded. Whether or not the legs were recorded as greenish yellow, yellowish green, grayish green or greenish buff (all color combinations of various breeding adults), the facts remain that yellow and green predominated in adults, that many third-year birds' legs were practically indistinguishable from those of adults, and that all first- and second-year birds were entirely different from adults.

In table 4, trends of leg colors are indicated for all age groups. It is of interest to note that there is a rough correlation between the color of the base of the bill and the color of the legs. This becomes apparent when one compares the data in figure 3 on bill colors with table 4 on leg colors.

Table 4

Seasonal and Age Variation in Leg Coloration

	First-year		Second-year		Third-year		Adult
July	blackish brown	Aug.-April	bluish white or pale greenish			Aug.-Dec.	bluish or yellowish green
Aug.-Feb.	pinkish white or brown			Aug.-Feb.	bluish white or green	Jan.-Feb.	greenish buff
Mar.-May	bluish white with pink tinge			Mar.-April	pale bluish green	Mar.-April	greenish buff or yellow
June-July	light greenish blue or bluish white	May-July	bluish green or pale yellowish green	May-July	pale bluish green or greenish yellow	May-July	yellowish green, yellow, or greenish yellow

Eyelid.—A summary of eyelid coloration by seasons and ages is presented in table 5.

Gape.—In a fashion similar to the color of the eyelid, the color of the gape varied seasonally and with age; a summary of the typical or usual color is given in table 6. By comparing these data with the tables for eyelid color and pigmentation of the bill, a general correlation becomes apparent. For example, adults in May have a vermilion gape, eyelid, and spot on the lower mandible.

In the Purple Finch (*Carpodacus purpureus*), Magee (1943) has shown by using birds over a period of years that in males the color of the gape changes from dull brownish in winter to bright red-orange at about the height of the breeding season. Sexual dimorphism was noticed in manifestation of this seasonal color; first-year males had red gapes but females did not.

Although somewhat less direct evidence is available than for the bill, probably the colors of the leg, eyelid and gape are also under androgenic control. Boss (1943) did not specifically discuss these structures as he did bill color and plumage characters, but, by stating that birds became mature in one year under testosterone injections, he indicated that these soft parts also attained the adult or mature colors. If vermilion may be considered as the ultimate or mature color attained by the eyelid and gape, adults reach this color seasonally (March or April) before third-year birds (May) and retain it much longer than do the third-year birds. This attainment and retention of the brighter coloration is probably correlated with androgenic titers.

Table 5

Seasonal and Age Variation in Eyelid Coloration

First-year	Second-year		Third-year		Adult	
blackish brown		blackish brown	Aug.-Feb.	yellow-orange or blackish brown	Aug.	orange-red or brownish orange
					Sept.-Feb.	dark red or orange-red
	April	yellow-orange to reddish orange	Mar. April-	dull orange-red or orange	Mar.	orange-red or vermilion
	May	orange-red	May	orange-red or vermilion	April-June	vermilion
	June-July	red or orange-red	June-July	red or orange-red	July	red or orange-red

Table 6

Seasonal and Age Variation in Gape Coloration

First-year		Second-year		Third-year		Adult	
Aug.	flesh-colored	Aug.-Sept.	flesh-colored or orange-yellow	Aug.-Mar.	orange or yellow-orange	Aug.-Mar.	orange-red
		Oct.-Mar.	yellow-brown or orange				
		April	yellow-orange or reddish orange	April	orange-red	April-May	vermilion
May-June	flesh-colored or dull orange	May	orange-red	May	vermilion		
July	flesh-colored	June-July	orange-red or yellow-orange	June-July	vermilion or dull orange-red	June-July	vermilion or bright orange-red

BURSA OF FABRICIUS

The bursa of Fabricius has been used rather extensively to determine the age of birds, particularly certain species of game birds. The bursa is prominent at an early age and generally disappears upon attainment of maturity of the bird (Hochbaum, 1942; Elder, 1946; Leopold, MS). The exact function of the bursa is not known, even though various workers have investigated the anatomy and physiology of this structure (see Linduska, 1943:427, for a discussion of this subject).

In the California Gull, measurements of the bursa were taken on most of the birds collected except for a period from July through September. The measurements were made by placing a millimetric rule against the outside of the bursa on the inside of the peritoneal cavity; the greatest length from the wall of the cloaca to the tip of the bursa was taken. The results of these measurements as correlated with age are presented in figure 4.

Although for a given month the bursae of first- and second-year birds might not be significantly different in length, the graph does show a general trend toward virtually complete atrophy of the structure by the time the gulls are in adult plumage. Certain discrepancies arise in the third-year and adult groups, such as absence of the bursa in some third-year birds and its persistence in some adults. As a general rule it was found that third-year birds of both sexes that were believed to be breeding had smaller bursae than did the nonbreeding birds of this age group. Out of fourteen third-year birds (May, 1953), seven were believed to be breeding, and, with the exception of one bird with a 10 mm. bursa, all had bursae less than 6 mm. On the other hand, out of the seven nonbreeders all except two had bursae at least 8 mm. in length. Similarly, in the Canada Goose (*Branta canadensis*), Elder found that wide variation in the rate of bursal regression was an indication that geese do not all reach breeding condition at the same age. Probably the gulls in adult plumage that still retained a bursa were birds four or five years old, but, of course, it was not possible to determine the age of these birds after the third year.

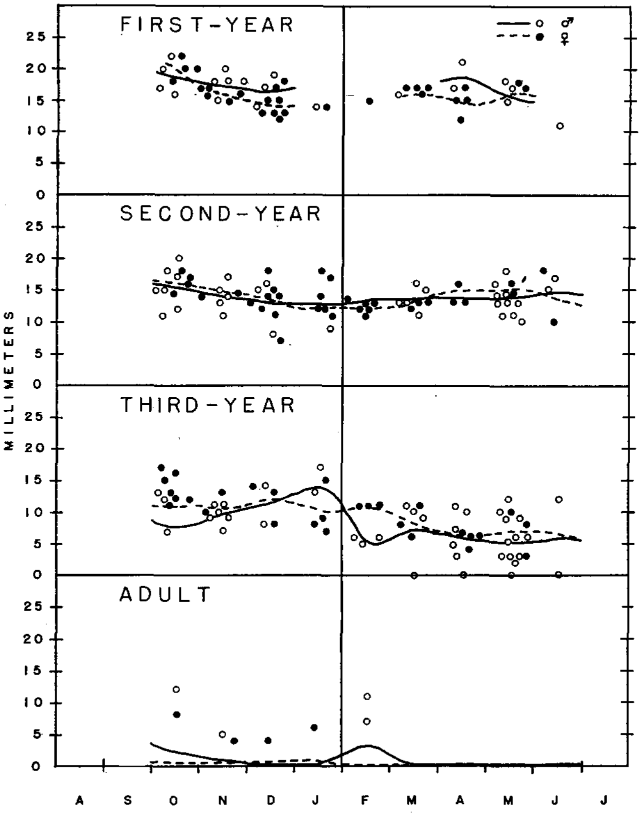

Fig. 4. Length of the bursa of Fabricius. Lines represent mean monthly values. Of 122 adults examined, only the 8 which had a bursa are plotted on the graph.

Hormonal control of the bursa has been worked out in the Ring-necked Pheasant by Kirkpatrick and Andrews (1944). They concluded that in the male, testosterone is responsible for the involution of the bursa while in the female stilbestrol induced the same involution. Direct evidence of hormonal control is lacking for gulls, but, as will be discussed in detail later, there are several facts which indicate a greater androgen output in adults than subadults, especially during the breeding season.

TESTIS CYCLE

SIZE

A customary criterion for avian reproductive condition has been the degree of hypertrophy of the testes. This enlargement may be determined in a number of ways by measurement. Since the testes of both breeding and nonbreeding gulls were found to be ellipsoid in shape, volumetric determination derived from linear measurements was considered to be sufficiently accurate. The formula for the volume of an ellipsoid was used: $V = 4/3\ \pi ab^2$, where $a = \frac{1}{2}$ longest diameter and $b = \frac{1}{2}$ shortest diameter. In 222 birds both testes were measured immediately after the birds were shot in the field and before fixation; in a few instances when one testis was damaged by shot, only the undamaged testis was measured. In most previous studies only the left testis has been measured, and, from the results of measuring both testes of 222 California Gulls, this would seem to be a valid procedure (see table 7).

Table 7

Comparison Between Volumes of Left and Right Testes

	Number	Per cent
Left testis larger than the right	188	84.7
Right testis larger than the left	19	8.6
Testes equal in volume	15	6.7
	222	100.0

Riddle (1918) and Friedmann (1927) have considered the problem of testicular asymmetry in birds, and Riddle, working with pigeons, thought that an excess of males in a population was always correlated with proportionately larger left testes. Friedmann presents evidence from many species collected at random showing that this is not true of wild populations. The data for the California Gull support Friedmann's conclusion. As will be discussed in a later section, practically a 50–50 ratio of adult males and females was obtained at the Mono Lake colony and yet, as table 7 indicates, the greater percentage of males has the left testis larger than the right. Friedmann further indicates that in two species of the Laridae (both terns) the testes were equal in size, but he did not examine any *Larus*.

Cycle for migratory birds.—The graph of testicular enlargement for the California Gull is plotted on a semilogarithmic scale in figure 5. The range and number in each sample are given in table 8. Generally the mean volume of the left testis is larger than that of the right testis. For the critical months of April and May when the data were available, semimonthly means for third-year and adult birds have been calculated. These semimonthly divisions were considered to be desirable because in April the first half of the monthly sample includes premigratory birds from the San Francisco Bay area whereas the second half includes recent arrivals at the breeding colony at Mono Lake. The sample from the first half of May includes birds at a time just after most of the eggs in the colony had been laid, and the second-half sample is comprised of birds taken just before eggs hatched in early June.

Table 8

Testis Volume for All Monthly Samples

		Left			Right		
Age group	Month	Number	Range in mm.^{3}	Mean	Number	Range in mm.^{3}	Mean
First-year	August	10	2.1– 16.5	9.3	9	1.3– 10.5	7.3
	September	2	11.5	11.5	2	8.4– 11.4	9.9
	October	6	8.4– 10.5	9.4	5	6.3– 8.4	7.1
	November	4	8.4– 13.6	10.5	2	8.4– 10.5	9.5
	December	2	9.4– 10.5	10.0	2	5.9– 7.3	6.6
	January	3	6.3– 9.4	8.0	2	7.3– 13.1	10.2
	February	0			0		
	March	2	8.4– 10.5	9.5	2	4.1– 8.4	6.3
	April	1	16.4		1	16.4	
	May	5	10.5– 28.3	16.6	5	5.3– 13.1	9.3
	June	0			0		
	July	1	9.4		1	8.4	
Second-year	August	4	8.4– 23.6	17.2	4	6.3– 10.5	8.7
	September	5	8.4– 19.8	13.1	5	1.6– 8.4	5.9
	October	7	8.4– 28.3	15.2	7	6.3– 18.9	11.6
	November	5	9.4– 16.4	12.1	5	5.3– 14.7	9.4
	December	2	14.7– 26.0	20.4	3	8.4– 10.5	9.8
	January	2	4.7– 16.4	10.6	2	3.5– 13.1	8.3
	February	1	8.4		1	3.5	
	March	5	18.9– 50.4	28.5	5	11.4– 35.2	21.4
	April	0			0		
	May	5	85.1–1157.2	719.6	5	54.4–1013.7	569.0
		4	28.3– 419.2	262.7	3	26.0– 256.6	129.1
	June	3	207.9– 385.6	292.0	3	104.8– 189.0	144.6
	July	0			0		
Third-year	August	4	11.5– 30.7	19.5	4	9.4– 16.3	12.3
	September	7	8.4– 104.8	33.5	7	8.4– 33.2	13.9
	October	6	9.4– 26.0	13.1	6	6.3– 23.6	12.6
	November	5	8.4– 38.5	22.8	5	7.3– 23.6	13.5
	December	1	18.0		1	9.4	
	January	2	19.8– 23.6	21.7	2	7.3– 9.4	8.4
	February	3	19.8– 32.1	26.7	3	9.4– 18.9	14.9
	March	4	32.1– 54.4	42.5	4	21.2– 38.5	31.1
	April	3	38.5– 244.8	112.6	3	54.4– 118.1	75.6
		3	402.2–2053.1	1198.7	3	282.4–1204.5	774.8
	May	7	806.0–2258.9	1321.8	7	502.9–2156.0	956.1
		6	502.9–1140.7	796.8	4	486.4– 890.0	675.0
	June	7	282.4– 714.8	470.3	7	117.9– 636.5	330.2
	July	6	90.2– 594.0	252.1	6	58.7– 308.0	140.3
Adult	August	7	48.1– 158.4	96.9	7	32.1– 141.4	67.2
	September	4	58.7– 67.0	63.0	4	28.3– 46.0	37.4
	October	5	23.6– 41.7	29.1	5	21.2– 50.4	29.4
	November	5	16.4– 102.9	57.4	5	16.4– 50.4	32.8
	December	5	46.0– 111.4	71.7	5	38.5– 91.8	57.3
	January	3	78.8– 150.9	102.8	3	58.7– 91.8	78.5
	February	5	26.0– 98.3	65.0	5	21.2– 79.5	42.5
	March	5	54.4– 680.0	309.2	5	71.2– 419.2	204.0
	April	2	256.6– 410.6	333.6	2	150.9– 282.4	216.7
		3	2357.3–3281.0	2743.7	3	1659.2–1770.6	1703.8
	May	10	942.8–2882.6	2007.7	9	1013.7–2053.1	1568.2
		5	295.4– 785.0	463.9	5	131.0– 550.8	351.3
	June	12	67.0– 321.0	160.3	12	78.6– 254.5	119.0
	July	9	58.7– 368.8	135.3	9	38.5– 134.7	83.1

During the first year there is no noticeable increase in size of the testes until about the middle of May at which time there is a small increase. This enlargement might have occurred in April, but not enough data are available for that month. This increase is not correlated alone with the breeding season because this slightly greater testis volume is maintained at approximately this same level (between 10 and 20 mm.^{3}) during the second winter.

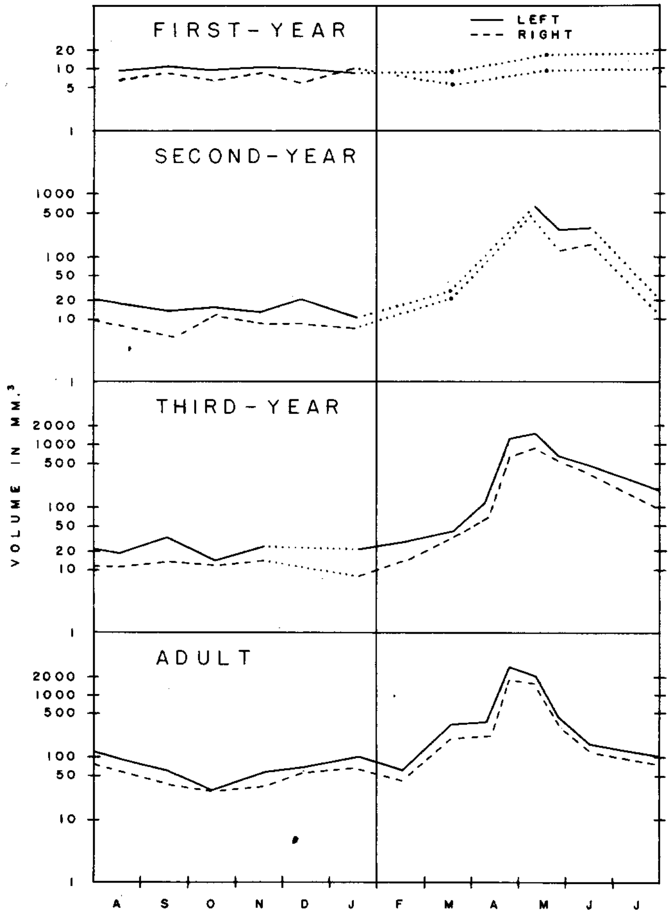

Fig. 5. Semilogarithmic graph of cycle of mean testis volume. Dotted lines represent suspected trends when a monthly mean was not available.

Beginning in late February, or more likely early March, second-year birds show a noticeable increase in testis size. Although no sample of second-year birds was obtained in April, apparently birds in the middle of May at the breeding colony reach the greatest testis size for this age group. At this time adults already had eggs in their nests (see fig. 1). It will be seen that these second-year birds reach a maximum testis volume somewhat later than adult birds, and they involute rapidly until the winter minimum size is reached by August when the birds have returned to the San Francisco Bay area. This mimimum size may be reached in July, but no data are available for that month.

During May second-year birds show a very wide variation in testis volume, from 28.3 to 1357.2 mm.^{3} (left) and 26.0 to 1013.7 (right). This wide variation (see table 8) is believed to be correlated with different degrees of maturation even within a given age group. There is no evidence that any first- or second-year birds breed.

The winter monthly averages of testes for birds in their third year are somewhat higher than for birds in the second year. At the end of February and the beginning of March, there is another rapid increase in testis volume, but, on the average, third-year birds' testes are about twice as large as the testes of second-year birds in the first part of May. It is of considerable importance to point out that there is about a ten-fold increase in testis volume between premigratory and migratory birds of this and the adult age group in April, and that the maximum testis size for the third-year birds is found in the first half of May, somewhat later than in adults. As will be discussed in more detail later, some third-year males breed, and in five cases out of seven the testes of such breeding birds were larger than those of nonbreeders at the colony. Size of the testis, however, is not the only factor to be considered because all of these birds, nonbreeders included, had spermatozoa in their testes. I believe that, on the average, subadult breeding occurs a little later than adult breeding, but there is little documentary evidence for this in the California Gull. This phenomenon is known to occur in some passerine birds (see, for example, Baldwin, 1953:334–337).

After involution of the testis, the minimum winter size in adults is reached in October. Adult testes are season-for-season larger than testes of any of the other age groups. Following the spring enlargement, which begins at least by mid-February, the maximum size is apparently reached at the end of April (or perhaps the first week or so in May), a size which is larger than the average for third-year birds at the same time, but there is still an overlap in measurements between these two age groups. Adult testes begin to involute immediately after the eggs are laid in early May, since smaller testes are recorded for mid-May.

The general seasonal picture of testicular enlargement for this gull is similar to those reported for other species of birds. In both the first-year Starling (Bullough, 1942) and the Fulmar (Marshall, 1949) the maximum testis size in spring is smaller than that for adults. The sharp peak of enlargement in the gull is correlated with the single brood raised, whereas in passerine birds which are known to be at least double-brooded (for example, English Sparrow, Keck, 1934) a plateau of testis size is maintained for two or more months.

Rollin (1944) presents some figures for winter testis size in *Larus argentatus, Larus canus* and *Larus ridibundus*. During a period from November to February adult testes were one-half again as large as those in first-year birds. A few second-year birds had testes intermediate between these two age groups. The left testis was almost always larger than the right. The greatest difference in size between left and right testes was found in adult birds, whereas in first-year birds there was a smaller difference between the two testes. All these data are in agreement with the results of testis size presented in figure 5 for the California Gull.

Cycle for nonmigratory birds.—Due to the general scarcity of California Gulls along the Pacific coast during the breeding season, only a small sample of nonmigratory birds was obtained. There is a tendency for these nonmigrants to be widely dispersed, with less tendency for flocking and attraction to the local garbage dumps. A total of fifteen nonmigratory males was collected in the San Francisco Bay area in the seasons of 1952 and 1953, and the volumes of the testes of these birds are presented in table 9. By comparing this rather small sample with the data from birds which migrated to the breeding grounds (fig. 5 and table 8), it is seen that the volumes for first-year birds are probably not significantly different, although only one bird was available for June and July at the breeding colony. At this time the testis volumes of nonmigrants indicate an increase similar to the sample in May of migratory first-year birds, and this volume is maintained as the approximate winter average for second-year birds.

Table 9

Testis Volume of Nonmigratory Birds

	First-year		Second-year		Third-year		Adult	
Date	Left	Right	Left	Right	Left	Right	Left	Right
May 6, 1953			67.0	54.4				
June 4, 1952	9.4	8.4	79.5	32.1				
	23.6	12.6						
June 26, 1952	10.5	6.3	16.4	8.4				
	10.5	18.9						
July 5, 1953	16.4	18.9						
	8.4	9.4						
	8.4	6.3						
July 21, 1952			28.3	8.4	21.2	23.6		
July 30, 1952	18.0	10.5					67.0	51.3
	8.4	7.3						

The testis volumes of nonmigratory second-year, third-year and adult birds during May, June and July are all significantly smaller than volumes for migratory individuals. With the data available it is difficult to explain why some individuals in the same age groups should develop large testes and migrate to the breeding colony while others remain in an undeveloped state and do not migrate. This would suggest a different response to the photoperiod by the pituitary-gonad mechanism which is associated with migration. At some point in this chain of events, certain individuals do not respond, but at what point and for what reason has not been ascertained.

Random collecting at the Great Salt Lake and Mono Lake colonies shows that there is a greater tendency for the older age groups to return to the breeding colonies than for the younger birds to do so, and most of the subadults which do return do not breed. Table 10 shows the numbers of each sex and age collected at these two colonies (data from Great Salt Lake from Behle and Selander, 1953:257). Furthermore, the information for nonmigrants is in agreement, because progressively fewer older birds were taken in the San Francisco Bay area during the breeding season.

Table 10

Numbers of Birds Collected During the Breeding Season

	Great Salt Lake		Mono Lake	
	Males	Females	Males	Females
First-year	3	0	6	4
Second-year	41	19	12	5
Third-year	43	4	29	4
Adult	19	18	40	38

Young Herring Gulls banded by Gross (1940) at Kent Island were obtained there again at all ages: first-year, 1; second-year, 6; third-year, 7; and adults, 28. A significant point which correlates well with observations at Mono Lake is the fact that (p. 147) "a few individuals in the first nuptial plumage are also to be seen at the colony during the breeding season. However, the breeding gulls discourage the presence of these younger birds and it is not an uncommon experience to see these dusky visitors violently driven away from the nesting area."

As Behle and Selander concluded, these data also indicate that in the subadult groups males are more numerous at the breeding colony than are females. The cause for this is not known, but it is probable that males tend to mature earlier than females. Further evidence for this comes from observations of subadult breeding of certain males but not of females and from soft-part colors which are more like adults in third-year males than in females. There is no reason to believe that females are elsewhere in the region of the breeding colony because no groups or individuals of nonbreeding birds were ever observed anywhere in the vicinity of Mono Lake other than at the colony.

TUBULE SIZE

By determining the mean size of the seminiferous tubules, it has been possible to show that there is a direct correlation between size of the tubules and size of the testis. Sections from 177 left testes were examined and the mean diameter of 10 tubules selected at random was calculated. Only tubules that were cut in perfect transverse sections were measured with the ocular micrometer. Sometimes faulty fixation or some physical distortion of the tubules rendered the section and the slide unusable for this particular phase of the study; thus, all 222 males were not examined. When more than one bird of a given age group was available for the month, a mean of the measurements from the birds was determined.

Table 11

Mean Tubule Diameter in Millimeters

Age group	Month	Number of birds	Range	Mean
First-year	August	5	.045–.058	.053
	September	2	.050–.058	.054
	October	5	.046–.053	.049
	November	4	.035–.050	.045
	December	2	.041–.051	.046
	March	2	.043–.051	.047
	May	3	.064–.067	.066
Second-year	August	3	.045–.053	.049
	September	5	.043–.054	.049
	October	7	.045–.051	.049
	November	5	.043–.048	.045
	December	3	.047–.048	.048
	January	1	.044	
	February	1	.044	
	March	5	.061–.072	.067
	May	8	.069–.202	.145
	June	1	.149	
Third-year	August	3	.042–.060	.051
	September	7	.046–.063	.052
	October	6	.042–.053	.045
	November	5	.040–.050	.046
	December	1	.054	
	January	2	.048–.054	.051
	February	3	.058–.063	.061
	March	4	.069–.076	.071
	April	5	.070–.194	.128
	May	8	.149–.212	.177
	June	2	.129	
	July	3	.080–.121	.093
Adult	August	7	.048–.061	.055
	September	4	.050–.055	.053
	October	5	.048–.056	.052
	November	5	.052–.062	.057
	December	5	.048–.056	.051
	January	3	.054–.059	.057
	February	5	.053–.065	.060
	March	6	.069–.111	.083
	April	5	.125–.178	.144
	May	7	.072–.201	.136
	June	6	.066–.094	.076
	July	6	.061–.085	.069

Table 11 summarizes the data on tubule size, and it can be seen that the tubule diameters follow the same general enlargement as the testes (table 8). A more detailed analysis of this type was carried out by Blanchard and Erickson (1949:274) on the White-crowned Sparrow (*Zonotrichia leucophrys*). One would not expect a perfect correlation because there are other variable constituents of the testis-intertubular cells, blood vessels and tunica albuginea. Except for first-year birds the larger tubules are found during the breeding season in all age groups, and the smaller tubules during the nonbreeding seasons.

Just as in testis size, tubules of second-year birds during the breeding season are enlarged but are not as large as those of third-year and adult birds. Also, the maximum tubule size of second-year and third-year birds occurs in mid-May, but adults reach their maximum size in late April. Although the data show a larger breeding tubule for third-year birds when compared with adults, these two age groups probably are not significantly different. Similar results have been reported for the White-crowned Sparrow (Blanchard, 1941:57) and British Starling (Bullough, 1942:177).

HISTOLOGICAL STAGES OF SPERMATOGENESIS

At least one testis from each of 249 males was prepared for microscopic examination. After fixation in Bouin's fluid, dehydration was accomplished with dioxan. Paraffin sections were cut at 10 micra, and these were stained with Delafield's or iron hematoxylin and counter-stained with eosin. Only a small portion of the larger testes was sectioned, usually a part from one end.

The histological details of spermatogenesis have been worked out for several species of passerine and a few species of nonpasserine birds. Those passerine species which have been investigated include the English Sparrow (Loisel, 1900–1901), White-crowned Sparrow (Blanchard, 1941; Blanchard and Erickson, 1949), Starling (Bullough, 1942), Oregon Junco (Wolfson, 1942), and Red-winged Blackbird (Wright and Wright, 1944). In the broad features of spermatogenesis, all these species are in close agreement, although some differences of opinion have arisen relative to defining and delimiting the stages or steps which lead to the production of spermatozoa. The males of several of these species breed in their first and subsequent years, there being essentially no differences in spermatogenesis between first-year and adult birds. Many larger, nonpasserine species, however, such as the Fulmar (Marshall, 1949), do not breed until more than one year old, and the meager data for such subadults have indicated that their spermatogenesis might differ in some way from that of adults. On the other hand, the Ring-necked Pheasant (Hiatt and Fisher, 1947) and probably some other large nonpasserines mature and breed by the end of their first year; the breeding cycle of the first-year individual in these types is the same as that of the adult.

Several specific points regarding spermatogenesis in the California Gull need to be indicated. It has been necessary to describe anew the stages of spermatogenesis for this species because of its long maturation period, but these stages are roughly comparable to those used by Blanchard (1941). More stages, but relatively fewer details for each stage, are given for this gull so that it might be possible to determine more accurately exactly how far in spermatogenesis the subadults proceed before regressing. The interstitial cell cycle is not included with the spermatogenic cycle as other authors have done because the two cycles are not always "in phase" in a given month for any two age groups. For example, even at the height of the breeding season adults that have mature spermatozoa also have numbers of interstitial cells rated as "common" whereas third-year birds with spermatozoa have only "fairly common" interstitial cells. The interstitial cell cycle in adults, however, correlates closely with the spermatogenic cycle.

Stage 1: Inactive condition; primary spermatocytes (fig. 6*a*).—In the inactive winter condition the testes are at a minimum size, and the tunica albuginea is of maximum thickness. There is a basal row of spermatogonia and Sertoli cells next to the basement membrane. A small lumen is almost always present.

One of the most interesting characteristics of the inactive gull testis is the presence of primary spermatocytes in all sections examined. They lie for the most part toward the lumen from the spermatogonia and form a more or less complete row of cells, but occasionally they may be wedged between

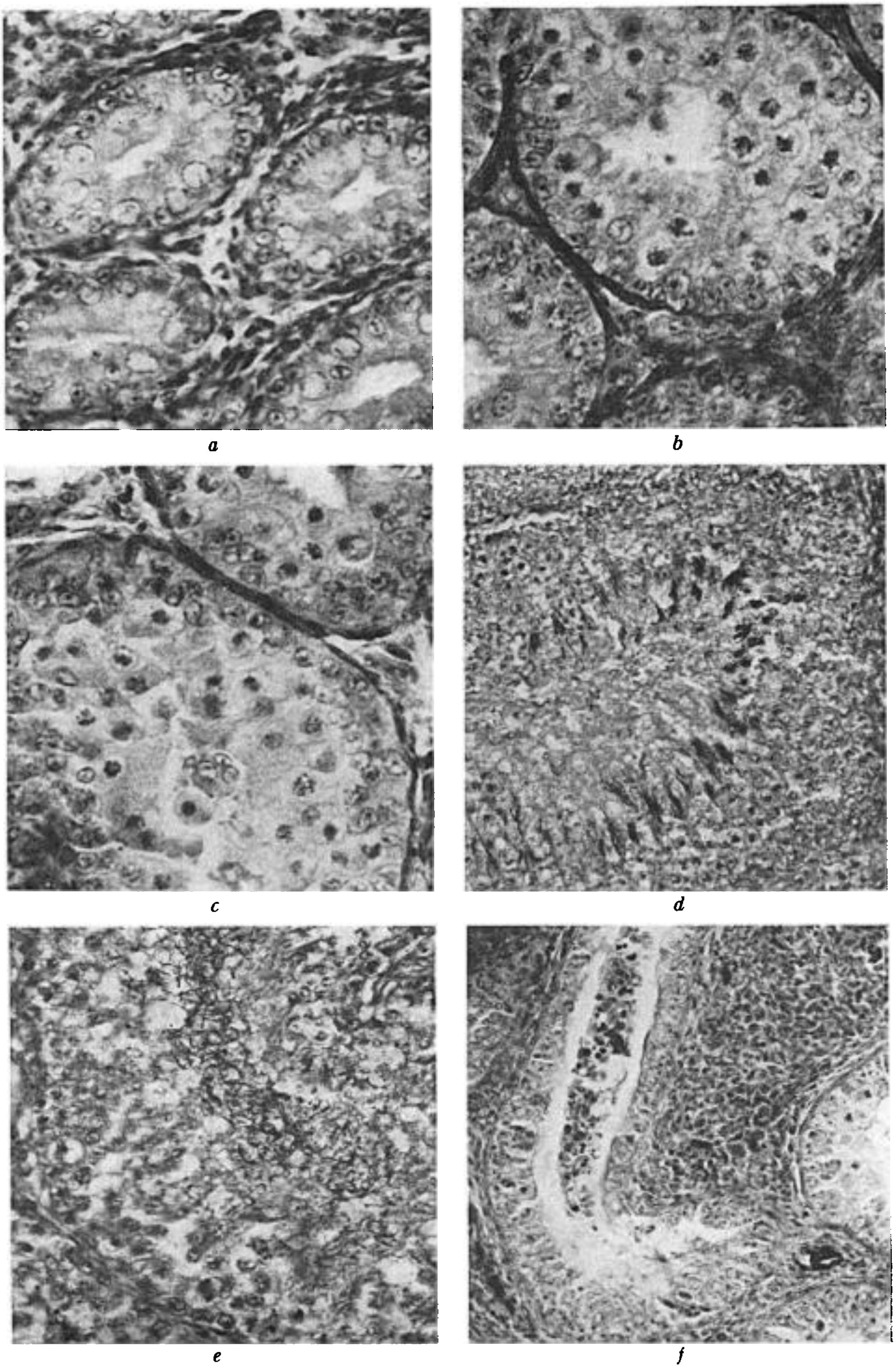

Fig. 6. Sections of testes of California Gulls showing representative histologic stages. *a*, stage 1, inactive condition; *b*, stage 3, primary spermatocytes in synapsis; *c*, stage 4, secondary spermatocytes; *d*, stage 6, breeding condition; *e*, stage 7, spermatozoa in lumen; *f*, stage 8, regression. *a-c*, approximately ×580; *d-f*, approximately ×270.

spermatogonia in the basal row. Probably these are the same cells that Loisel (1900–1901), Wolfson (1942) and other authors have described and figured as spermatogonia of the second order, but it seems more correct to call these cells inactive primary spermatocytes. Evidence to support this contention comes from at least two sources. In the first place, in the late summer and early fall when birds-of-the-year have primary spermatocytes in synapsis, it is noticeable that they are being derived from and pushed inward from the basal row of spermatogonia. In midwinter in this age group, when synapsis in the primary spermatocytes disappears, the size and position of the now-inactive cells are the same as for the primary spermatocytes in synapsis at an earlier time. In fact, they might be the same cells. In the second place, these inactive spermatocytes are of the same size, shape and position as primary spermatocytes in synapsis which appear at the advent of spermatogenesis in the early spring. Hiatt and Fisher (*op. cit.*) noted that Ring-necked Pheasants also have spermatogonia and primary spermatocytes at all times of the year. This stage is equivalent to stages 1, 2, and 3 of Blanchard.

Stage 2: Primary spermatocytes in synapsis.—There is still basically one row of spermatogonia and Sertoli cells, but there may be some increase in the number of these cells, especially if a long stage 1 (that is, of winter duration) preceded this stage. (Exception to this statement is to be found in first-year birds in the summer and early fall when their testes are of minimum size with no apparent increase in number of any cells; a short stage 1 would have preceded this condition.) Up to about one-half of the primary spermatocytes in a given cross section of a tubule have their chromosomes in synapsis, and frequently the chromosomes lie at one side of the nucleus. As in stage 1, these primary spermatocytes form an incomplete row of cells next to the lumen. The lumen is sometimes filled with detritus. Blanchard's stage 4 is an equivalent stage, except that the tubules in the gull are not noticeably larger than those of the preceding stage.

Stage 3: Increase of primary spermatocytes in synapsis (fig. 6*b*).—The tubules begin to enlarge, and the tunica albuginea becomes thinner as the entire testis enlarges. Primary spermatocytes in synapsis have increased in number to the extent that (1) the majority of them are in synapsis and (2) they usually form two or more rows next to the lumen, moving away from the basement membrane. This is similar to Blanchard's stage 5, except that testes with secondary spermatocytes are not included in this stage. Wolfson (1942:253) does not regard this as an adequately delimited stage, at least in the White-crowned Sparrow and Oregon Junco, but in gulls it was easily separable from stages 2 and 4, although one stage grades into another.

Stage 4: Secondary spermatocytes (fig. 6*c*).—The second part of Blanchard's stage 5 included the presence of secondary spermatocytes, but in the gull this stage may be recognized as distinct. Perhaps, in the White-crowned Sparrow, Blanchard should have recognized a separate stage for secondary spermatocytes because between her stage 5 (predominance of primary spermatocytes in synapsis plus a few secondary spermatocytes) and stage 6 (spermatids) there was an unaccountable gap in testis volume between 13.0 and 19.7 mm.^{3} This stage and the following are not as frequent as the other stages in gulls, but this is probably because they are of shorter duration.

Stage 5: Spermatids.—Most of the spermatids border the lumen, but a few metamorphosing ones are seen moving away from the lumen toward the Sertoli cells. Only rarely are mature spermatozoa present, these being in negligible numbers. Spermatids are in relatively small numbers when compared to the number of primary spermatocytes. This was even true in testes in stage 6. This condition stands in marked contrast to the testes of some passerine species in which spermatids may occur in several rows bordering the lumen (see, for example, White-crowned Sparrow, plate 11 of Blanchard, 1941). Since only a few birds were found in this stage, it is probable that not only is the stage passed through rapidly but also that sampling of migratory and premigratory birds at the correct time was inadequate.

Stage 6: Spermatozoa in bundles: breeding condition (fig. 6*d*).—Testes and tubules are at maximum size in this and the next stage; also, the tunica is thinnest. Spermatozoa are present in a large number of bundles which are spaced around the tubule; they may be in several rows. Much cellular debris is present in the lumen. Only occasionally are the spermatozoa seen in the lumen, but evidently some quantity of them must have already passed down the reproductive ducts because birds with testes in this stage were seen in copulation at the breeding colony. Furthermore, by the time the majority of the adults reached the following stage (May 15), most of the eggs in the colony had already been laid.

Stage 7: Spermatozoa in tubular lumen (fig. 6*e*).—This stage differs from stage 6 because here the majority of the sperm bundles have been shed into the lumen of the tubule. Much detritus is also present in the lumen. This may be the beginning of regression because in some subadults the testis is beginning to decrease in size. Adult testes, however, reach their largest average size in this stage (table 8), and there is no noticeable collapse of the tubules. For these reasons stage 7 is regarded as a separate stage from regression.

Stage 8: Regression (fig. 6*f*).—Other authors have not always considered regression in a spermatogenic study, but in any treatment of an annual cycle of gonadal events, it must be taken into account. After the spermatozoa are shed into the lumen, this event is followed by the casting off, in succession, of spermatids, spermatocytes and probably spermatogonia and Sertoli cells. This entire phenomenon of regression is considered here as a single stage. Large masses of necrotic cells and cellular debris are found in the lumen, and the tubules collapse. At the same time, at least some spermatogenesis is still going on because primary spermatocytes in synapsis are evident. Toward the end of regression, only a few cells may be found in the lumen while a basal layer of spermatogonia, Sertoli cells and usually a few primary spermatocytes remain. It is likely that the primary spermatocytes which are found in the winter inactive testes are derived from spermatogonia at the end of regression. This is also the period when the collapsed tubules are becoming smaller, approaching the inactive winter condition.

Figure 7 summarizes the annual cycle of spermatogenesis for the four age groups. In approximately one-half of the gulls, both the right and left testes were examined, but, since no significant differences were found between the two testes, only the left testis was sectioned thereafter. There is a strong tendency for individuals of the same age on the same day to have testes in the same spermatogenic stage, especially in third-year and adult birds. Some of the second-year birds, however, are more variable, especially at the height of the breeding season.

Examination of the data for first-year birds in late summer and fall suggests that some spermatogenic activity is taking place at that time. The presence of primary spermatocytes in synapsis (stage 2) was a condition indistinguishable from that of testes at the advent of spermatogenesis in the spring. None of the other age groups showed this out-of-season spermatogenesis. A partly different condition of precocious sexual development has been reported for the English Sparrow in which species Davis (1953) found a few juveniles which were sexually mature in June and early July. This condition was attributed to the probable fact that these birds had been hatched in late winter and were subsequently brought into sexual activity by the pituitary responding to increasing day length. Some birds even had primary spermatocytes in September. The explanation for sparrows in June and early July is inappropriate for the first-year gulls because the latter were collected from August through October when the day length was shortening. A situation suggesting spermatogenic activity similar to that in the first-year gull has been noted in juvenal Ring-necked Pheasants by Hiatt and Fisher (1947:538–539). From September 15 to October 7, all the birds-of-the-year examined by them were in an advanced stage of spermatogenesis, and three birds even had spermatozoa.

Although only a small sample of first-year males was taken at the Mono Lake colony during the breeding season, all the evidence points to the fact that birds of this age group which return to the breeding colony never have testes beyond stage 3. Similarly, first-year male British Starlings were found by Bullough (1942:178) to have only primary spermatocytes in synapsis during the breeding season. This incomplete spermatogenesis would provide an obvious reason for nonbreeding in this age group.

Spermatogenesis in second-year birds at the breeding colony was somewhat intermediate between that of the nonbreeding first-year birds and the breeding adults. As has been mentioned previously, there is no evidence that any second-year birds in this species ever breed, but the fact that many such birds are at the breeding colony with spermatozoa in their testes presents a peculiar situation. These would be potentially breeding birds, but I believe this gonadal condition is the only known feature of this age group which may be considered mature. Birds of this age with their browner plumage and less bright soft parts must be recognizable as such to adults, and it is probable that they are not accepted as mates because of these differences. On several occasions at the Mono Lake colony, second-year birds were seen to alight amid the eggs and young of adults, but they were soon driven off by the nearby adults.

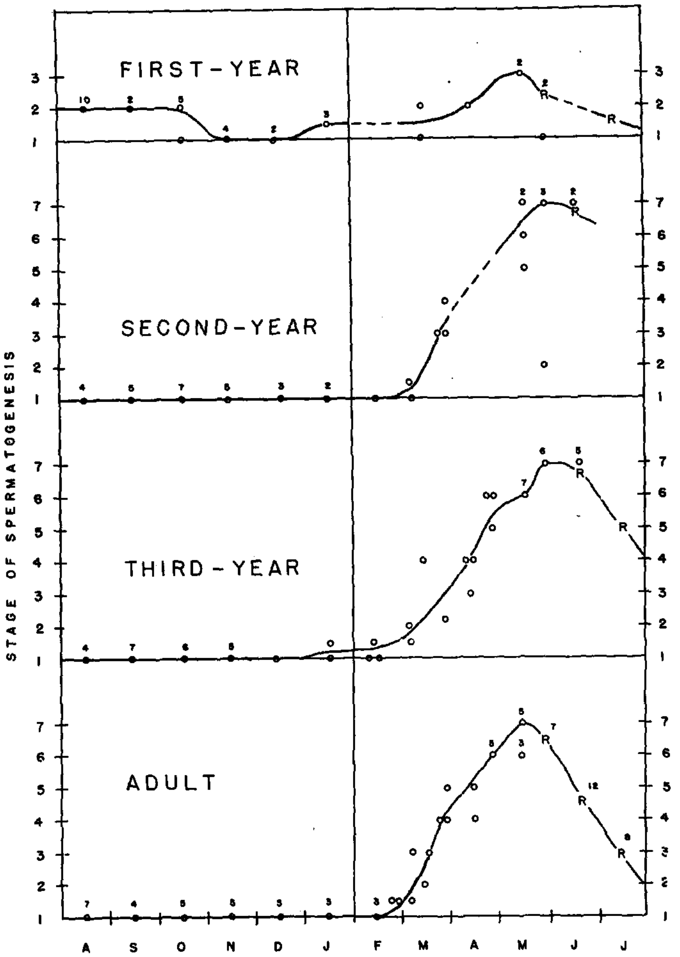

Fig. 7. Cycle of spermatogenesis. The solid line represents a mean value, and the broken line a suggested trend when data were not available. Regression is indicated by "R."

One might wonder, then, if the second-year birds interbreed, but again there is no evidence that this occurs in the California Gull. Although males of this age group might have spermatozoa, and are thus potential breeders, among the females it can be shown that the ovary is not yet producing enlarged follicles. In the Glaucous-winged Gull (*Larus glaucescens*), Jones (*fide* Bent, 1947:67) observed that some immature birds of unknown age were breeding apart from the main colony of breeding adults.

There were two puzzling second-year males (fig. 7) which, during May at Mono Lake, were in incomplete stages of spermatogenesis (stages 2 and 5). In the same age group, why should some birds be so much more advanced in spermatogenesis than others? The answer to this question seems to be that even in one age group there are degrees of maturity. Some second-year birds also approach the adult characters of plumage and colors of soft parts more than others. These degrees of maturity are probably also reflected in sex hormonal titers.

The spermatogenic cycles for the third-year birds and adults are essentially the same except that there seems to be a tendency for the adults to begin regression sooner. A possible explanation for this might be that the few third-year males which breed do so a little later on the average than do the adults. This is also indicated by the fact that adults on the average reach a given stage of spermatogenesis even away from the breeding colony before the third-year birds. Apparently, most, if not all, of the third-year birds and adults completed spermatogenesis. At least, no birds were taken during May and June which were not in stage 6 or 7 or regressing from these.

Even though it was not possible to follow and collect birds all the way from the coast to the breeding grounds in the spring, it can be shown that adults reach at least stage 5 before arriving at the breeding colony, and it is possible that at least some birds have spermatozoa when they arrive. This is shown by the fact that all adults taken at the end of April had spermatozoa even though some birds were still migrating into the Mono Lake area. On the other hand, third-year birds prior to reaching the breeding colony were in stage 4, and at least one bird after arriving at the colony did not have spermatozoa. In certain passerine species (for example, Oregon Junco and White-crowned Sparrow) birds at the onset of migration have less developed spermatogenic stages than does the California Gull.

Although there is a general correlation between size or volume of the testis and stage of spermatogenesis in some species of birds, in the gull sufficient overlapping of stages in one age group and variations in volume in the same stage from one age group to another occur to make inaccurate the use of size of testis as an indicator of spermatogenesis.

Nonmigratory males.—Nine first-year birds were taken in June and early July (see table 9), and, with the exception of one bird in stage 3 and beginning to regress, all were in stage 1. A second-year bird on May 6, 1953, was in stage 5, and three others in this age group in June and July were in stage 8. Only one each of a nonmigratory third-year and adult bird was taken; these were obtained in late July when regression was nearly complete. No spermatozoa were seen in any of these testes.

These few records cannot be used as conclusive evidence in relating spermatogenesis to migration, but certain inferences might be drawn. As far as the first- and, perhaps, second-year birds are concerned, there does not seem to be a significant difference in spermatogenesis between nonmigratory and migratory individuals. In regard to first-year birds, I cannot agree with Behle and Selander (1953:246) that "perhaps the lack of development of the gonads is correlated with poor development of the migratory instinct. . . ." The first-year birds which they collected, and also the ones in the present study had poorly developed gonads and yet had migrated to the breeding colony. Apparently some factor or factors other than the mere development of the gonads are more closely related to migration in these first-year birds.

[Part II dealing with the other aspects of the reproductive cycle and a summary will appear in The Condor in a later issue.]

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