THE REFRACTORY PERIOD OF TESTIS RHYTHM IN BIRDS AND ITS POSSIBLE BEARING ON BREEDING AND MIGRATION

BY A. J. MARSHALL[1]

ACCORDING to Burger (1949: 222) the "problem of refractoriness is perhaps the greatest relatively unsolved problem in reproduction." Actually, except in ultimate detail, the problem may have been solved (Marshall, 1949a; 1950a). The "refractory period" of Bissonnette (1931; 1937) and certain other authors is here defined as that period of the avian testis cycle when the tubules are in a state of post-spermatogenetic lipoidal metamorphosis and before the newly regenerated Leydig cells of the interstitium have become sufficiently lipoidal and mature to respond to neurohormonal influences *initiated by natural factors in the environment.*

The term *neurohormonal* as used in this paper refers to the interaction of the exteroceptors, the hypothalamus, the anterior pituitary, and the gonads. The term *lipoid* has, of course, no precise chemical meaning, but used histochemically in its widest physical sense, it includes fats and all other animal substances that, in solubility, resemble fats (see Baker, 1946). It is hardly necessary to emphasize that the interstitial and tubule lipoids mentioned above have no direct connection with the gross deposits of peritoneal and subcutaneous fat that Wolfson (1942; 1945: 125) avers is a diagnostic concomitant of readiness to migrate.

The period of testis reorganization described above varies in duration from species to species. While it is in progress the post-moult summer and autumn sexual display, described for many passerines and other birds, occurs.

Internal Rhythm of the Testis

Before discussing in detail the refractory phase of the testis in relation to the breeding cycle and to light-experimentation which has been carried on since Rowan's (1925) remarkable pioneer discovery, it is best to see the phenomenon in its true perspective within the gonad cycle. In the young bird the inactive tubule contents are free of lipoids (Fig. 1). The interstitium contains juvenile Leydig cells that exhibit cholesterol-positive lipoid droplets which increase in quantity until many of the cells reach an almost maximum size at a time when the contents of the adjacent spermatogenetic tubules (and the bird's plumage in some species) also indicate approaching sexual maturity.

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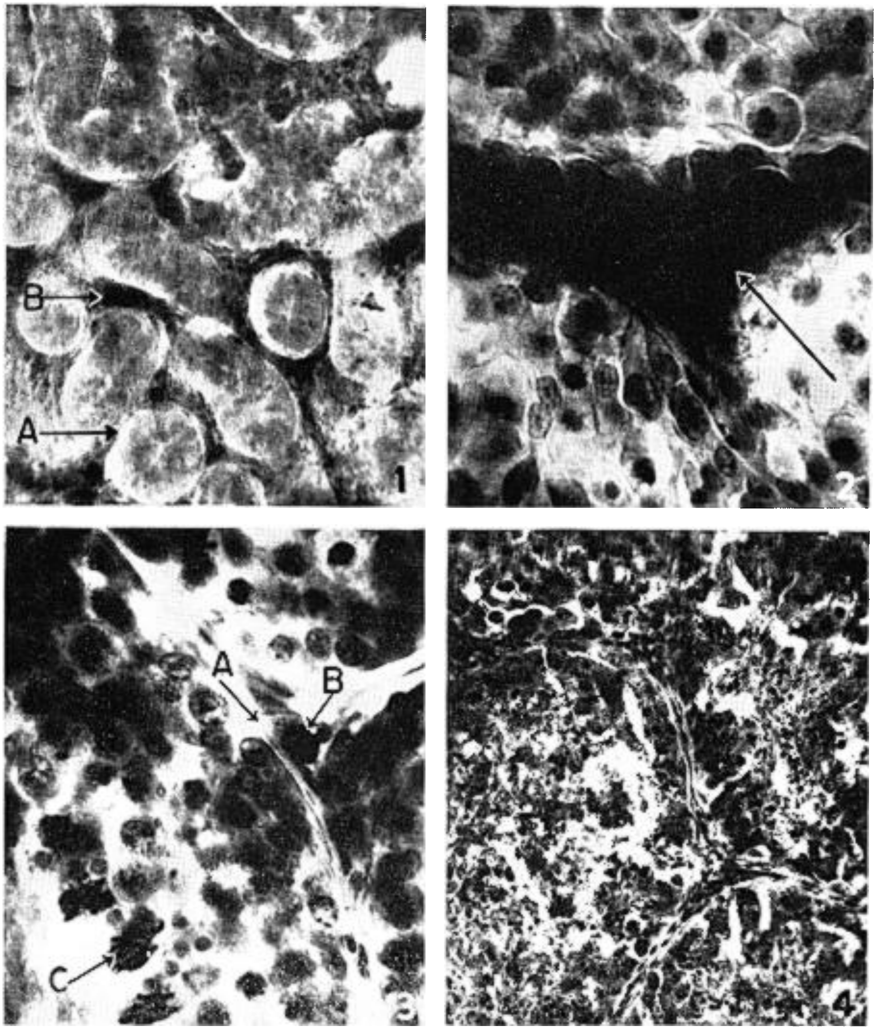


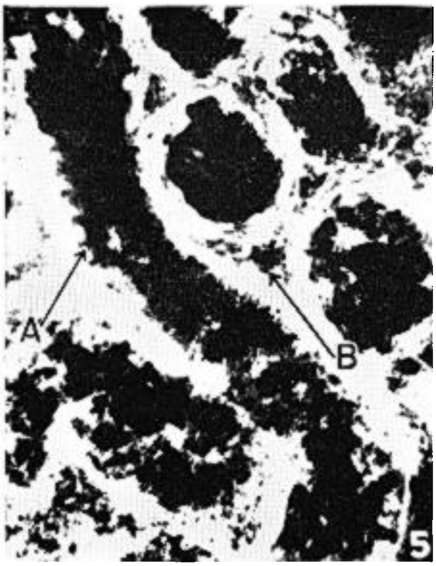
Photomicrographs of avian testis sections. (Formal-calcium fixation and Scharlach R. colouring with Ehrlich's haematoxylin counter-staining; 15μ.)

FIG. 1. Rook, aged 11 months. × 300. A. Inactive spermatogenetic tubule. B. Tract of Leydig interstitial cells gaining in lipoid content.

FIG. 2. Adult Rook taken at about the same season as Fig. 1. × 650. Arrow indicates typical wedge of heavily lipoidal Leydig cells at a time when the first mature spermatozoa appeared in adjacent tubules.

FIG. 3. Adult Rook approaching height of spermatogenesis. × 600. The great expansion of the seminiferous tubules has dispersed the Leydig cells, which are losing their lipoids and cholesterol. A. Leydig cell devoid of lipoids. B. Leydig cell still heavily sudanophil. C. Bunched spermatozoa.

FIG. 4. Adult Australian "Magpie" (*Gymnorhina dorsalis*) that has undergone interstitial exhaustion, shed spermatozoa, and entered the refractory phase. × 320. The small black spots within the tubules are the first evidence of tubule steatogenesis. Postnuptial tubule breakdown has begun.



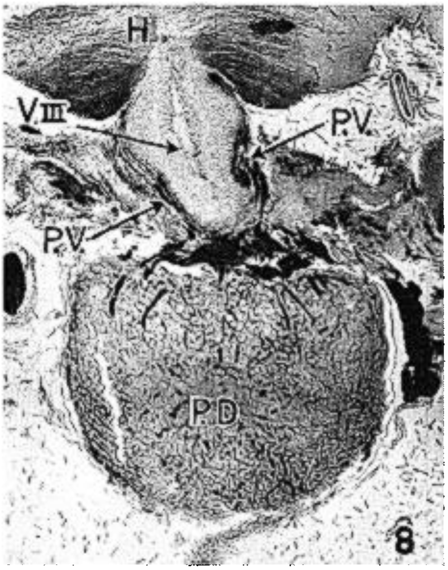


FIG. 5. Adult Rook testis in postnuptial phase of tubule metamorphosis and interstitial regeneration. × 350. A. Collapsed tubule full of cholesterol-positive lipoids. B. Group of juvenile, lipoidal, cholesterol-positive Leydig cells. (Technique as in Figs. 1–4.)

FIG. 6. Adult Rook testis as collapsed during refractory period. × 400. Note necrotic sperm debris within tubules. (Bouin fixation, iron haematoxylin, at 7μ.)

FIG. 7. Adult *Gymnorhina dorsalis* testis at stage comparable to that of Figs. 5 and 6. × 110. Arrow points to new testis wall inside old one. Testis regeneration is well under way and the refractory period is almost at an end. (Technique as in Fig. 6.)

FIG. 8. Hypophyseal portal system of adult Rook. × 25. H. Hypothalamus. V. III. Third ventricle. P. V. Portal vessels. P. D. Pars distalis of anterior pituitary. (Formal-calcium and Lepehne-Picworth method at 40μ.)

In the sexually quiescent adult the interstitium generally consists for the most part of comparatively small lipoid Leydig cells. These contain fuchsinophil elements which are readily seen after the soluble lipoids are removed by embedding in wax. As the sexual season heightens, the Leydig cells increase in size and lipoid content. Varying in quantity and arrangement from species to species, considerable aggregations of heavily lipoidal Leydig cells can now be seen (Fig. 2). The ripening spermatogenetic products expand the seminiferous tubules and this causes a wide dispersion of the clustered Leydig cells so that few are found in any given microscopic section. At the height of spermatogenesis, and at the beginning of lipoidal metamorphosis of the germinal epithelium, the Leydig cells become almost exhausted of their lipoid content (Fig. 3). An increase in the number of mitochondria may be seen in their cytoplasm (Benoit, 1927; 1929). Soon a fuchsinophil cell appears in which it is not possible to demonstrate the presence of cholesterol. There is a difference of opinion concerning the relative function of the lipoid and the fuchsinophil cell. Sluiter and van Oordt (1947; 1949) call the latter (which has also a vacuolated form) the "secretory cell" and declare that it manufactures the sex hormone. Marshall (1949a) on the other hand, considers the lipoid cell the site of hormone production and believes that the fuchsinophil cell is essentially a lipoid cell that has run its cycle and is about to disintegrate or to give rise to another generation of juvenile Leydig cells.

Concurrently, when the tubules have reached their maximum size and after spermatozoa are shed, some tubules undergo a lipoidal metamorphosis (Fig. 4). (This is quite distinct from the lipophanerosis observed during vertebrate spermatogenesis and described in all histology textbooks.) Soon the contents of all tubules become almost wholly lipoidal (Figs. 5 and 6). The tubules rapidly collapse as the necrotic spermatozoa and other debris clear away. Meanwhile, a new generation of small juvenile Leydig cells arises in the spaces between the shrunken tubules (Fig. 5) and the interstitium is invaded by new blood vessels. There now arises a prolific growth of fibroblasts which build up a new *tunica albuginea* (Fig. 7) inside the distorted and fragile old wall; the new Leydig cells become meagerly lipoidal and fuchsinophil; and eventually these become sufficiently mature to respond to external stimuli via the pituitary gland: the refractory period is ended.

The reorganization referred to above is often associated with the postnuptial moult and is probably responsible for the brief period of sexual quiescence that now ensues. Further, experimental birds cannot now be forced into spermatogenesis by increased illumination. It is not yet known to what extent testis rehabilitation is influenced by the secretion of pituitary gonadotrophins in free-living birds. Miller (1949), for example, has shown that in late October (long after the initial stages of rehabilitation) large daily injections (1 cc. = 50 international units) of pregnant mare serum quickly caused testis enlargement in wintering Golden-crowned Sparrows (*Zonotrichia coronata*) that were probably still refractory to photostimulation. Among free-living birds the tubule-lipoids disappear and the new interstitium matures at different rates from species to species. Although this writer believes that the gonad is the primary organ of periodicity, the anterior pituitary too may have a refractory phase. However, no anatomical evidence that such is the case has yet been adduced.

The postnuptial tubule lipoids are cholesterol-positive. In many bird species a sustained period of autumnal display, song, and territorial behavior begins as the postnuptial tubule lipoids disintegrate and the new interstitium develops. The tubule lipoids may, during their postnuptial existence, have an endocrine function, but this has not yet been proven.

The above metamorphosis, even though it involves testis collapse, cannot be termed simply a "regression" since it involves the rehabilitation of the interstitium, the tubules and the testis tunic. Until the tunic has been rebuilt and the Leydig cells renewed, the next spermatogenesis cannot, of course, occur. The metamorphosis, in addition to the subsequent "spring" development of interstitium and seminiferous tubules, constitutes the physical basis of the internal rhythm postulated by F. H. A. Marshall (1936) and Baker (1938a) in their classical reviews on sexual periodicity and the evolution of breeding seasons.

It should be mentioned that interstitial Leydig cells appear to be present throughout the life of the bird. Authors have sometimes considered these cells absent because inappropriate techniques have removed the cytoplasmic lipoids and thus rendered the cells unidentifiable.

Experimental Photostimulation and the Refractory Period

Since Rowan's epochal discovery that photostimulation led to testis-response in the Junco (*Junco hyemalis*), many other birds have been found to respond in the same way. It is unnecessary here to refer specifically to the several excellent reviews of the work on the effects of light duration, light intensity, and the components of light on captive birds, or to the various ingenious experiments of Benoit in trying to determine the neural pathway by which light from the environment finally leads to the activation of the hypophysis. There seems no reason to believe that sunlight and other external stimuli conducive to breeding do not achieve a nervous threshold which leads to the stimulation of the anterior pituitary via the hypophyseal portal system that is present in birds (Fig. 8) as well as in various other animals (Popa and Fielding, 1930; Houssay, *et al.*, 1935; Wislocki and King, 1936; Green and Harris, 1947; Harris, 1948). Avoiding the "light versus metabolic activity" controversy, we can say, in general, that if seasonal birds are subjected to additional rations of artificial light outside the refractory period their testes will enlarge.

In the light of the above demonstration of the anatomical basis of the refractory period, several previously puzzling aspects of photostimulation can be readily understood. Bissonnette and Wadlund (1932: 345), commenting on the "failure of the sex mechanism to maintain a high rate of germ-cell multiplication and maturation beyond a definite period," state that "the more stimulating the effect of the illumination, the more quickly is the mechanism thrown out of gear." There seems little doubt that the above workers, and many others, experimentally drove the birds through their spermatogenetic and interstitial cycles to sexual exhaustion and, not understanding the mechanism involved, called the subsequent period of reorganization (when the testis was temporarily unresponsive to further stimuli) the refractory period. It is interesting that both Rowan (1929) and Bissonnette (1930), who worked with traditional wax-section techniques, remarked on the presence of tubule vacuoles at the post-spermatogenetic stage. Rowan in particular mentioned that these "vacuities" appeared as though artificially produced; but he emphasized that they were not artifacts. He was, of course, correct: they are the empty spaces left where the metamorphosed fats have been dissolved out of the sections after wax embedding.

It will be recalled that Riley (1936; 1937) found that the testes of adult House Sparrows (*Passer domesticus*), though unresponsive to photostimulation in September were responsive in November. By November (in the Northern Hemisphere) postnuptial reorganization has proceeded sufficiently to allow the testis to respond. Likewise, Riley's success in stimulating juvenile birds in September is understandable when we realize that their tubules, never having produced spermatozoa, have not metamorphosed, and their lipoid Leydig cells are still developing and are therefore receptive to the stimuli of additional lighting. It becomes clear, too, that there is nothing remarkable in the experimental production of more than one spermatogenesis in a year; and the histophysiology of the ancient practices of *yogai* (Miyazaki, 1934) and *mewing* (Damsté, 1947) can be readily understood.

Seasonal Stimuli after the Refractory Period

We can now consider birds as free-living animals in touch with all of the varied stimuli that keep their breeding cycles in step with the seasons and ensure for their young an arrival time suitable for survival.

After the breeding season there is among some British birds an almost general recrudescence of singing, courtship display, and other forms of sexual behaviour which may continue into autumn and winter (Morley, 1943). Again, in North America, the Mockingbird, *Mimus polyglottos* (Michener and Michener, 1935), Song Sparrow, *Melospiza melodia* (Nice, 1937), White-crowned Sparrow, *Zonotrichia leucophrys* (Blanchard, 1936), Wren-tit, *Chamaea fasciata* (Erickson, 1938), Ring-necked Pheasant, *Phasianus colchicus* (Hiatt and Fisher, 1947), and other species have been reported to exhibit varying degrees of sexual activity in the autumn. In some British species, notably the House Sparrow, Starling (*Sturnus vulgaris*), Wood Pigeon (*Columba palumbus*), Stock Dove (*C. oenas*), Robin (*Erithacus rubecula*), and Blackbird (*Turdus merula*), this characteristic post-moult activity may occasionally lead to autumn reproduction (Witherby, *et al.*, 1948) if weather and food conditions remain propitious. It is noteworthy that some of these occasional autumn breeders exhibit pronounced autumnal sexual activities in North America (Witschi, 1935; Allard, 1940).

Bullough (1942) has shown that in England testis-size in the Starling begins to increase in September. This is accompanied by autumnal sexual activity. Höhn (1947) has histological evidence that autumnal interstitial development in the Mallard (*Anas platyrhynchos*) is followed by mating behaviour.

In three British species—the Rook (*Corvus frugilegus*), Robin, and House Sparrow—the relation of autumnal sexual activity to internal testis rhythm has been studied. The Rook (Marshall and Coombs, unpublished) ovulates in March in Cornwall; the testis tubules rapidly metamorphose and the interstitium begins to regenerate while incubation is still proceeding. Males shot whilst carrying food to the young in the nests possessed collapsed tubules heavy with lipoids and an interstitium already regenerated with Leydig cells meagerly lipoidal and correspondingly responsive to the Schultz test for cholesterol. After this rapid testis reorganization there appears to be a comparative lull in development. The tubules lose their lipoids very slowly and the Leydig cells appear not to develop further. Meanwhile moult has begun. By the end of June the young birds flock separately and require no further attention from the parents. With the testis tubules still lipoidal and with moult proceeding, a new *tunica albuginea* is being laid down in readiness for the next enormous expansion of the organ. By the end of August wing and tail feathers have been replaced and the new testis wall is complete. There are still plenty of metamorphosed lipoids in the tubules but a new growth of spermatogonia is present beneath them and almost all of the necrotic sperm debris has been eliminated. Also, there is a slight increase in the size and lipoid content of the Leydig cells.

It is now that the Rooks renew their "mating flight" and many start carrying sticks to their old nests. Most, if not all of the characteristic spring courtship behaviour occurs, including, occasionally, copulation (Morley, 1943). In a small number of males, testis development begins in September and culminates in complete spermatogenesis in October. It is remarkable that in the great bulk of a given rookery there is no considerable change in the testes. Despite the extraordinary—and regular—sexual resurgence described above, Rooks almost never actually reproduce in the autumn. During a normal winter the testes that do develop begin to metamorphose when sexual activity dies down in November. "Spring" gonad development begins in December at about the winter solstice or a little later. The time of onset varies among individuals and also from year to year according to the weather. Study of the female sexual cycle is still in progress.

The above detailed data about a single species are given here because they have an important bearing on the question of the validity of photoperiodic stimulation of birds in nature. Among many species sexual behaviour occurs after the regeneration and partial development of the interstitium, whether the days are lengthening or shortening. When the moult is concluding and the young are able to care for themselves (or even before), postnuptial sexual behaviour may become very pronounced depending upon the weather and the traditional habit of the species. This appears to be essentially controlled by the internal rhythm of the gonad. In southwest Britain both the Robin and the Rook breed earlier than in the north, the former also beginning its autumnal song and territorial aggression (Lack, 1939), the latter also its autumnal sexual display, earlier. If autumn weather conditions (especially sunshine) and food supply are good, autumnal sexual behaviour is extremely pronounced. In the Robin it may lead to reproduction in a few individuals (Lack, 1946). The chief point to be emphasized is that though light is decreasing sexual activity is increasing. It is not until November, when the sun is rarely seen, when weather conditions are worsening considerably and food is becoming scarce, that sexual activities are inhibited. It has been suggested that autumnal sexual activities are depressed when day-length falls below a certain number of hours, but there appears to be no good evidence that mere shortness of day is responsible. Other environmental factors seem to be far more important.

Again there seems to be no sound evidence, apart from that obtained through photostimulation experiments in cages, that the onset of "spring" sexual activity is correlated directly with any precise day length. There has been no widespread histophysiological investigation of the gonads in the winter period when many spring-breeding species begin their seasonal spermatogenesis. Data about to be published reveal that at Oxford, England, the Robin, a spring-nesting bird, exhibits an interstitial rearrangement and a sudden growth of Leydig cells in the first week of January. There is at the same time a marked revival of song. Pairing takes place. This occurs after a light-increase of approximately 12 minutes from the winter solstice, when day-length is increasing at the rate of about one minute per day. Before it can be unquestionably accepted that light fluctuation causes the above prenuptial sexual recrudescence, far more elegant experimental techniques than those used in the past will have to be devised.

The Starling, on which much photostimulation work has been done, is of great interest here because of the detailed histological study by Bullough (1942). Burger (1949) reports that the minimum day-length required by this species for the rapid production of spermatozoa is about 12.5 hours, and that days 10.5 hours long produce only the multiplication of spermatogonia. But under unusually mild winter conditions in Britain, Starlings will not only produce spermatozoa but will nest, ovulate and bring out viable young when the days are little more than nine hours long. Further, an analysis of Bullough's data shows that under natural conditions a "great burst" of testicular growth occurs at the beginning of February when the days are only about 9.3 hours long, and that by the end of the month the first sperms have appeared when the days are about 10.6 hours long. Spermatogenesis is reported to have continued rapidly although day-length was still little more than that which Burger was later to claim could produce only the multiplication of spermatogonia. These facts are brought forward to show how far from reality can be the most carefully planned and regulated photoperiodicity experiments.

So much for light and the *initiation* of the prenuptial part of the breeding cycle. What, now, of ovulation? Summarizing an important survey (which of necessity dealt with selected species having wide geographical ranges) Baker (1938b: 578) stated: "6. Much egg-laying occurs when days are getting shorter, and indeed it often proceeds rapidly while they are decreasing in length and only between 11 and 12 hours long.

"7. There is, however, little egg-laying when the day is shorter than 11 hours, and almost none when it is less than 10.

"8. Under natural conditions birds exhibit no tendency to start breeding everywhere when the days reach a certain length nor when they are becoming longer particularly quickly."

There is ample evidence that the timing of ovulation in a given species, even in the same locality, has no direct relationship with day-length. Records kept by the Marsham family in Norfolk, England, for the past two centuries reveal that the first appearance of young Rooks varies from 23 March to 2 May (Williams, 1949). There are numerous published data (*cf.* Marshall, 1949b) indicating that the breeding season fluctuates according to the mildness or severity of the weeks preceding nesting. When it became known that the British winter of 1946–47 was one of the coldest on record it was thought worthwhile to collect the gonads and stomach contents of a small series of four common Oxford passerines—the Robin, Chaffinch (*Fringilla coelebs*), Great Tit (*Parus major*), and Blue Tit (*P. caeruleus*)—in mid-March in the hope that the following winter would be normal and the same species might be obtained in precisely the same wood exactly one year later. The winter of 1947–48 was unusually mild; the proposed second collection was made. The experiment was designed to rule out day-length as a factor and to test the effects of possible weather fluctuation.

There proved to be a great disparity between the gonads taken after the "hard" winter and those collected after the mild one. From March 13 to 15, 1947, none of the four species showed a greater development than primary spermatocytes in synizesis, whereas those collected exactly one year later had all reached secondary spermatocyte stage, and three of the four species had developed spermatids or spermatozoa. Analysis of weather and breeding records showed that the hard winter was followed by an abnormally bright spell (after the collection date) and that the surviving birds of at least three species bred at about the normal time! It is, of course, extremely difficult to evaluate such factors as sunshine, temperature and food abundance. Great care was taken to provide an adequate food supply for all birds collected in both winters. So, unless some special food component was operative, it seems that sunshine and temperature must have been particularly influential in the timing of the cycle.

Evolution and Timing of the Breeding Cycle

The ultimate factor (Baker, 1938a; 1947) in the evolution and timing of the breeding season is reproduction at a time of year propitious for the rearing of the young and thus also for the survival of the species. Secondly, there are *proximate* or immediate factors in the animal's environment acting as regulators and operating through the exteroceptors, thus keeping the breeding rhythm anchored to the seasons. Animals that do not respond to the appropriate stimuli may continue to lose their offspring and thus pay the death penalty as species.

The above regulation may be achieved in either of two ways or through a combination of the two ways:

1. The sexual cycle, once the period of postnuptial reorganization (or "refractoriness") is over, is under the control of a complex of regulating factors that occur at approximately the same times every year and so, ultimately, the young are launched at about the same beneficial period each year.
2. There is a possibility that in many species (particularly migratory ones) the male cycle is timed principally by a fixed rate of gonad reorganization, i.e., the clearance of last season's metamorphosed lipoids from the spermatogenetic tubules and the building up of the secretory component of the interstitium. If this be so, migration and breeding activity could begin, irrespective of light duration, weather, or geography (e.g., among birds on the equator), after the Leydig cells had reached a certain threshold of hormone production. The sexual cycle, then, must be finally timed by the external immediate factors (presence of appropriate nesting sites, food, etc.) that permit successful reproduction when migrants or dispersive species reach their breeding grounds. The breeding cycle is still under the more or less rigid control of the environment and thus keeps step with the sun.

This second matter can be dealt with first. Bissonnette (1937: 257) has suggested that the breeding cycle and migration in some species might be governed by "inherent rhythms of the anterior pituitary more or less fixed in the absence of, or without responsiveness to, external, usually stimulating, factors like light cycles." Previously, however, Baker and Baker (1936: 517) had expressed their belief that "if in any plant or animal there were an internal rhythm controlling an annual cycle, and if this rhythm were incorrect even to the minute extent of six minutes in the year, then if it were breeding in the spring at the end of the last glacial epoch in the northern hemisphere it would be breeding at precisely the wrong season of the year (autumn) now!" From what is known of the time factor in biological reactions any such exactitude is inconceivable; furthermore, there is as yet no evidence that the anterior pituitary is autonomous in its activity. F. H. A. Marshall (1936; 1942) and Baker and Ransom (1938: 103–105) have, however, pointed out that certain Southern Hemisphere birds appear to adhere to their southern breeding times after transportation across the equator even though the majority soon adjust to the new environment. Thus, it would seem clear that some birds possess an internal rhythm of reproduction. Baker (1938a) has suggested briefly that some such rhythm may prevent migratory European Swallows (*Hirundo rustica*) from nesting in the South African summer and that it may be influential in timing the return of migrants to their breeding grounds. The present writer, in view of material presented in this paper, suggests that a fixed rate and period of gonad reorganization may be influential in timing the departure of spring migrants. The testis tubules of certain waders in northern Africa are clear of lipoids and their Leydig cells are fairly constant in lipoid content at the time of their departure northward (Marshall, 1950b). The same is true of the Hooded Crow (*Corvus cornix*) before it leaves eastern England for its Scandinavian breeding grounds (Marshall and Coombs, unpublished). Passerine birds of eight species[2] so far investigated contain spermatozoa when they kill themselves against St. Catherine's Lighthouse, Isle of Wight, on their spring migration from Africa and southern Europe. This evidence reinforces Rowan's contention (see also Rowan and Batrawi, 1939) that the northern migratory journey is essentially sexual in motivation. It is difficult to see how the day-length hypothesis can explain the northern movement of birds that "winter" near the equator. Thus, of two individual Golden Plovers (*Pluvialis apricaria*) of the same subspecies, one may winter a little to the north, the other a little to the south, of the equator: the former exists under an increase of light, the latter under a decrease, yet both apparently arrive at their northern breeding grounds at approximately the same time. And if light is not influential, what other environmental factors are sufficiently constant over a wide area to be considered at all?

It seems certain that the urge to move towards the traditional breeding ground is inherent within each species, even as is the appreciation of the environmental pattern that allows for mating, ovulation and nidification when the birds get there. Even if migratory birds "winter" with potential mates in an area of abundant food, sunshine and prolonged day-length, other environmental factors essential for reproduction (e.g., traditional nest sites) are not present and therefore the cycle cannot be stimulated vigorously enough to bring about an unseasonal "autumnal" or postnuptial breeding condition. It seems possible, then, that in many migratory species there is a genetically fixed rate of testis recovery, and that when the rhythm has proceeded to a certain threshold any environmental stimuli (including behavioural interactions between the sexes) that influence the anterior pituitary can then be

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[2] Whitethroat (*Sylvia communis*), Blackcap (*S. atricapilla*), Willow Warbler (*Phylloscopus trochilus*), Pied Flycatcher (*Muscicapa hypoleuca*), Spotted Flycatcher (*M. striata*), Wheatear (*O. œnanthe*), Redstart (*P. phœnicurus*), and Sedge Warbler (*Acrocephalus schœnobaenus*).

operative on the now once more responsive gonads. Storr (1951) has recently described display in flocking Sharp-tailed Sandpipers (*Erolia acuminata*) in tropical Queensland (at Lat. 15° 22′ S.) in March and early April shortly before their departure for their arctic breeding ground. In the case of young birds, a fixed maturation rate may be the essential timing factor: once a certain sexual maturity is reached, environmental factors may be able to operate and to achieve a neurohormonal threshold sufficient to cause departure for the breeding ground. It will be recalled that when Emlen and Lorenz (1942) implanted sex-hormone pellets in free-living, sexually inactive California Valley Quail (*Lophortyx californica*), neighbouring, untreated birds also showed accelerated mating behaviour. In regard to this kind of sexual and social stimulation, F. Fraser Darling's "Bird Flocks and the Breeding Cycle" (1938) should be consulted.

The breeding rhythm of stationary Sooty Terns (*Sterna fuscata*) which are reported to breed about four times every three years on tropical Ascension Island (Murphy, 1936) is of outstanding interest. Here, apparently, the ocean environment contains sufficient quantities of food to allow more frequent successful reproduction than is usual in seasonal birds. Were this species an arctic migrant, such a rhythm would carry it north into an unpropitious climate and natural selection would operate swiftly and disastrously.

When migrants arrive at their traditional breeding grounds, the presence of an appropriate pattern of environmental stimuli allows them to breed and their reproductive cycle thus keeps step with the sun. In this respect the Great Skua (*Catharacta skua*) is noteworthy. It breeds widely throughout antarctic and sub-antarctic seas but a separate northern subspecies nests in Iceland (Huxley, 1950. *Discovery*, 11: 73–78). Although probably non-migratory, the Great Skua wanders north and south from its sub-polar breeding stations (James Fisher, personal communication). Both Huxley and Fisher have suggested that the northern population was established by nomads from the south. Thus we can visualize trans-equatorial wanderers covering thousands of miles of ocean and islands before finding northern quarters with an environment sufficiently like that at home to enable them successfully to breed and to found an arctic race.

A fixed rate of gonad recrudescence may explain some of the cases where, in certain restricted localities, two populations of the same species (sometimes, apparently, the same subspecies) co-exist and yet retain different breeding rhythms. Serventy and Whittell (1948) have reported separate winter and spring breeding populations of several species of sea-birds on islands off the west coast of Australia. In the case of the Silver Gull (*Larus novae-hollandiae*), two groups breed at different times on one small island. All colonies of Pied Cormorants (*Phalacrocorax varius*) but one breed in autumn and winter; the exceptional colony, on the Abrolhos Islands, breeds in the spring. On the other side of the continent, Barrett (1910) long ago noted that large numbers of

White-capped Noddies (*Anoüs stolidus*) on one Great Barrier Reef atoll had eggs on a certain date, while a second population, on a very similar island only 15 miles away, had not begun to lay.

In North America Blanchard (1941) and Blanchard and Erickson (1949) have shown that the gonads of two subspecies of *Zonotrichia leucophrys* living part of the year in the same area and exposed to the same day-lengths begin to enlarge at different times. Wolfson (1942) has interesting data of the same sort concerning races of *Junco oreganus;* and Bullough (1942) has shown that in Britain migratory populations of Starlings have different breeding cycles from those of non-migratory populations.

It seems probable that in temperate zone species such as the above there are environmental factors operating near the ovulation date and allowing of a successful mating when the habitat becomes seasonally appropriate for reproduction. Thus, too, it may be found that the external stimuli governing nidification and ovulation are the really important factors that keep the individual sexual cycles in step with the seasons rather than a long-range factor, such as day-length which is generally held to be the chief factor that anchors the sexual cycle in time.

Among certain birds inhabiting countries where the winter sky is usually overcast it seems that a principal long-range environmental influence is sunshine rather than mere length of day. An unseasonable burst of sunshine in winter will stimulate birds to sing; a spell of dull cold weather in spring will depress song and sexual activity. Inhibitory influences which prevent animals from wasteful unseasonal matings are sometimes as valuable biologically as stimulatory ones. A long succession of days suitable to reproductive development will heighten sexuality irrespective of day-length; and a period of adverse weather, even when days are lengthening, will depress it, thus delaying the sexual season. Sunshine may not play a great part in the timing mechanism of birds inhabiting countries whose winters are sunny; but the Oxford open-air experiment described above should make it clear that in dull-winter areas sunshine is important and that, furthermore, sunshine and day-length are not precisely the same thing. Much as an anthropomorphic parallel may be deplored, it is natural to cite *Homo's* feeling of exhilaration and general well-being in a mountainous or arctic region—even in subzero temperature—when the sun shines. The results of much of the photostimulation work can be explained in this way. If birds that have evolved a neurohormonal response to sunshine are subjected to electric or candle light (*muit*, *yogai*) it is understandable that the mechanism will be set in operation and that hypophyseal hormones will eventually reach and activate the gonads. In this context it can be recalled that the introduction of all sorts of alien substances into various parts of an animal will stimulate reproductive activity (F. H. A. Marshall, 1936). In the course of an investigation of a chicken disease, Asplin and Boyland (1947) observed that sulphonomide administration was followed by spermatogenetic activity and precocious sexual development (e.g., comb-growth) and sexual behaviour in week-old chicks.

Neither sunshine nor light-increase can be said to possess a stimulatory effect in the cycle of the Emperor Penguin (*Aptenodytes forsteri*), which brings out its young during the darkest, coldest, most tempestuous period of the year. On the other hand, the Adélie Penguin (*Pygoscelis adeliae*) of the same latitude hatches its egg during the lightest and warmest month, December. Levick (1914) has described the astonishing differential growth-rate of the two species—the "mushroom-like" development of the Adélie, which enables it to mature sufficiently to survive the following winter, and the slow growth of the Emperor chicks, which are carried about and warmed by their parents until the approach of better weather. We can only assume that *if* day-length has any influence on the rhythm of the Emperor Penguin, *decrease* in day-length is what stimulates its development. In this respect the carefully controlled investigation of Yeates (1949) demands consideration for it appears to prove (under very "natural" experimental conditions) that the autumnal reduction in daylight over a long (13–16 weeks) period somehow stimulates the oestrus cycle of Suffolk ewes to activity and to actual reproduction. Autumnal mating in sheep and in certain other mammals leads to a beneficial spring parturition.

Most birds hatch their young at a period when the days are long enough for obtaining the stupendous amount of food needed by the developing young. Also, when days are long the weather is so mild that the comparatively naked young are not frozen to death. Further, during the season of long mild days the food necessary for the young is at its maximum (Marshall, 1951: 270). But most of the evidence is against the probability that each species has evolved an exact relationship with its environment whereby, when the day reaches a certain length or when the sun arises at a certain time, its breeding cycle "ticks over" to launch the young at a specific time of the year. That daylight increment, allied with other factors, may be partly influential in timing the breeding cycle of some species cannot be denied; but the influence of this daylight increment has been grossly over-emphasized, and many of the photoperiodic manipulations designed to test its importance have been made under conditions having little correspondence with normal events in the lives of the birds involved.

We now know that most of the old travellers' tales of equatorial animals "breeding all the year round" are untrue. Individual tropical birds seem to have breeding seasons as sharp as those of the same families living in Tasmania, Sussex or Vermont. The Oxford University Expedition that established a laboratory for one year in the remarkably unvarying climate of the New Hebrides proved conclusively that the endemic race of the Golden Whistler (*Pachycephala pectoralis*) has as sharp a breeding season as that of another race in southern Australia (Baker, Marshall and Harrisson, 1940). In the New Hebrides (below the equator) the species ovulates when the days are growing shorter. In southern Australia (below the equator) it ovulates when days are growing *longer*. The same applies to other Australian birds living in approximately the same latitude as the New Hebrides. There is much other, though histologically less conclusive, evidence that birds living almost precisely astride the equator have sharp breeding seasons (Moreau, Wilk, and Rowan, 1947). Notable, too, is the fact that individuals of species which inhabit both sides of the island of Ceylon breed at different times of the year. The monsoon that brings rain to the southwestern side of the island comes at a different time from that bringing rain to the opposite side (Wait, 1931). The wide variation in breeding periods may be correlated with the monsoons.

A further argument against light in any form as an overall regulator is provided by the irregular cycles of many species of birds in countries where rainfall is scanty or spasmodic. Here, quite often, breeding dates are indubitably geared to rainfall or its immediate effects.[3] Carnaby (1946) states that northwestern Australian birds can be divided into several groups. Some (certain pigeons and quail and many passerines) breed at any time of the year following heavy rain. The seed-eating Budgerigar (*Melopsittacus undulatus*) and Zebra Finch (*Taeniopygia castanotis*) breed after the growing of grass following such rain. Certain species ovulate in a particular calendar month, but only if conditions are normal for the period. Finally, a few large birds of prey have a regular breeding time irrespective of environmental fluctuation. Serventy (1946) has an important account of spring-nesting Western Australian species breeding in autumn after heavy unseasonable rainfall. A little farther south, beyond the area of rainfall, there was no indication of unusual breeding. Robinson (1933) reports that the Dusky Wood-Swallow (*Artamus cyanopterus*) nests in the Western Australian autumn (when light is decreasing) if rain falls, and nests again in mid-winter if it rains again. Roberts (1937: 51) has collected evidence that in central Queensland Plum-headed Finches (*Aidemosyne modesta*) lay only when heavy rain brings on a good crop of grass with seeds; the finches begin building immediately the grass becomes long. Scrub-turkeys (*Alectura lathami*) in the same area begin raking rubbish onto their old incubators only after the first rains of the season. If the "wet" continues they will lay. In one season of abnormal rainfall these megapodes laid in wintertime. They rely, of course, on heat generated by the damp, decaying vegetation of their incubators to hatch the eggs. Makin informs the writer that in southwestern Queensland, where wet winters are exceptional, she observed several kinds of spring-breeding birds nesting before the winter solstice after unseasonable rain. In this respect, Orr's (1945) evidence concerning Galápagos finches (*Geospiza*) is of importance. Members of this genus apparently breed from mid-December to April during the wet season when in a wild state near the equator. In captivity in California, however, they generally nested from March

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[3] A. R. Phillips has reported that the Rufous-winged Sparrow (*Aimophila carpalis*) does not breed in Arizona in spring, but delays "until the summer rains" (see page 323 of this issue).

to November, the breeding period of most North American birds. If the captive equatorial finches had been, in fact, native species their breeding during March–July would no doubt be ascribed to day-length. It would seem that some xerophilous or other species, which have of necessity evolved a neuro-endocrinal cycle to respond to rain or its effects will breed at any time of year after a short postnuptial period of testis reorganization. A long, fixed period of reorganization would be fatal—the species would, perhaps, be refractory to external stimuli until long after the next rainfall and the passing of its beneficial effects. The above Australian references are mentioned because they are unfamiliar to most people; comparable data are available from other continents. Baker (1938a) in particular has gathered observations suggesting that the timing of breeding seasons is dependent on a wide variety of factors. There seems little reason to doubt that various species (or different populations of one species) have evolved a breeding reaction to entirely dissimilar environmental complexes and so enabled themselves to breed in all manner of habitats quite independently of the movements of the sun *per se.*

An invaluable method of inquiry into the causes of breeding season—and one that has not been seriously exploited—is the examination of environmental factors, or lack of factors, that inhibit breeding. Spasmodic non-breeding in birds and other animals is extremely common in all habitats subject to violent environmental fluctuations. Berney (1927) reported the complete inhibition of breeding of most species for 16 months in central-west Queensland. Manniche (1910) noticed that during one period many North Greenland birds failed to reproduce. He correlated the non-breeding of the Long-tailed Skua (*Stercorarius longicaudus*) with the absence of its normal food, the lemming. The observations of Schaanning (1916) in Novaya Zemlya, and of Pedersen (1930) and Løppenthin (1932) in East Greenland indicate that inhibition of breeding in the Long-tailed Skua, Pomatorhine Skua (*S. pomarinus*), and Snowy Owl (*Nyctea scandiaca*) is closely related to the lemming cycle which, as Elton (1924; 1942) has shown, occurs in a regular 3–4 year rhythm. When lemmings fail there is a widespread non-breeding among lemming-feeders. Marshall (unpublished) found that on the bleak, foggy island of Jan Mayen (east of Greenland) non-breeding in some species appeared to be caused by the lack of nesting sites safe from fox-persecution. Certain species that show no great conservatism in site-selection elsewhere nested almost entirely on lofty cliffs and pinnacles on this fox-infested island. Passage waders touched down in thousands but only a few remained through the summer and these did not breed. No wader has ever been recorded breeding on this island. Stomachs of the many waders shot by us contained only vegetable matter. The testes of summer males collected contained spermatozoa, so failure to breed may well have resulted from inability of the females to find the sort of food characteristic of the traditional nuptial area. Land and lake birds of many species have been reported from Jan Mayen by various expeditions, but only a very few breed there even though every day at the summer's peak provides 24 hours of light. The sun, however, rarely penetrates the heavy blanket of fog surrounding the island and most migratory and dispersive species do not find there an environmental pattern appropriate to their traditional reproductive needs. The only birds that breed freely are the cliff-nesting seafowl that can escape the fox population (which is confined to the island except during winters when the pack-ice allows egress across the sea to the Greenland coast) and that can find unlimited food in the surrounding sea. The testes of non-breeding species underwent the same spermatogenetic cycle as those of the breeding species, but in development lagged behind those of paired breeding birds. It seemed that both sexes of birds in a flock became potentially capable of reproduction but that lack of suitable external stimuli (e.g., those provided by a satisfactory breeding site and/or appropriate food) inhibited the final stages leading to fulfillment.

There is now abundant evidence that once the gametogenetic cycle of many birds is started off it is "kept on the rails" by a variety and a succession of immediate factors such as weather, display, food supply, nest-site availability, and so on. For example, the Australian Satin Bowerbird (*Ptilonorhynchus violaceus*) takes up territory and builds a bower and a display ground on which it places numerous decorative objects at about mid-winter (June) when light is decreasing or increasing at the rate of a few seconds per day (Marshall, 1950c). Within a month the male gonad has increased in size a hundredfold and bunches of spermatozoa have appeared. But the male continues to display to the female at the bower until late in September or early in October when the female goes off to build her nest. Nidification thus takes place when the forest becomes full of flying insects. It has been shown experimentally that bowerbirds are unable to seek out small insects that they do not see moving and that the fruit diet on which the adults largely subsist is inadequate to bring nestlings to maturity. Here, then, we have a complex mechanism involving an early taking up of territory but an actual nidification at a time suitable for survival of the young.

Another bird whose breeding cycle seems to be timed to culminate with the appearance of specialized food is the British Robin. As mentioned previously, this species pairs and its gonads begin their "spring" development in January. Spermatozoa appear within a month provided the winter is not excessively cold and sunless. Yet the female usually does not ovulate until April. Lack (1946) and Lack and Silva (1949) observed that at the time young Robins hatched the woods became full of food in the form of caterpillars. After the hard winter and subsequent abnormal sunshine of 1946–47, two broods that appeared before the bulk of the caterpillar harvest died "much below weight after a few days." In Oxford woods the leaves swarm with these caterpillars; and certain other species of birds which use them for their young also ovulate in time to take advantage of the harvest which ends in pupation about 12

June, plus or minus some days according to seasonal vagaries (John Gibb, personal communication). Species that feed on adult insects breed later. It seems certain that as the ecology of more species of birds is worked out in detail it will be discovered that a great number of them have cycles so timed that the incubation period ends when large amounts of animal food for the young are most easily obtainable. It is probably very significant that the various British birds that occasionally breed successfully in winter—e.g., the Wood Pigeon, Stock Dove, Robin, Blackbird, House Sparrow and Starling—get much of their food from human sources and have therefore become partially independent of the natural supply.

In many cases it may be found that the factors that time the production of the food also influence the sexual cycle of the potential breeders. These complex ecological relationships, including especially display and other behavioural interactions, present an exciting challenge to zoölogists of the future. It is clear that each vertebrate has its reproductive rhythm "anchored" in time by stimuli and inhibitors that are various and highly specific (Marshall, 1947). These will be determined only by the collaboration of workers in both laboratory and field. Both spheres of labour are equally important.

Summary

The refractory period in the testis cycle of seasonal male birds is that during which the seminiferous tubules are in a state of post-spermatogenetic lipoidal metamorphosis and before the newly-regenerated Leydig cells of the interstitium have become sufficiently mature and lipoidal to respond to neurohormonal influences initiated by environmental factors.

At the termination of spermatogenesis, most of the epithelial contents of the tubules metamorphose and disintegrate. The tubules themselves become reduced in diameter and the whole testis collapses. Concurrently, the exhausted Leydig cells of the old generation (almost denuded of their cholesterol-positive lipoids during the last stages of the sexual season) disappear. A new generation now arises in the spaces between the shrunken tubules. Fibroblasts appear in great numbers and rapidly build up a new *tunica albuginea* just inside the old testis wall (which has become thin, distorted and fragile). Thus, the period of testis collapse is also one of rehabilitation and not merely a "regression." *Postnuptial metamorphosis* is a more suitable term. The period during which the above profound changes take place is one of sexual quiescence. It is also the period of the postnuptial moult.

In late summer and autumn, after testis reorganization has proceeded to some degree and while the tubule lipoids are disappearing and the new interstitium is becoming lipoidal, many species have a characteristic postnuptial display. This behaviour seems to be initiated by events within the testis cycle. Environmental stimuli (including interactions between the sexes) may sometimes lead to a second reproduction when light is decreasing in duration and intensity.

It is known that the sexual cycles of some species are carried forward by sunshine and depressed by its absence. After their postnuptial metamorphosis, birds that have evolved a neurohormonal response to sunshine will respond sexually to candle and electric light—hence the ancient practices of *yogai* and *muit*, as well as some results of recent experimental photostimulation. While it is not denied that day-length *per se* may be partly influential in the timing of the breeding seasons of some temperate zone species, more refined techniques than those used in the past must be designed to prove it. Much photo-experimentation has been carried out under conditions that correspond but little with normal events in birds' lives. The exteroceptor/hypothalamus/pituitary/gonad mechanism of male birds may be easily jolted into activity by photostimulation, but the current theory that day-length is the most important factor in the initiation of the "spring" spermatogenesis (which often occurs at about, or shortly after, the winter solstice) is far from satisfactory.

The author believes that the internal gonad rhythm is the most important single factor in the timing of breeding seasons and the migration that is part of them. Thus, after varying periods following birth or reproduction, many species seem to be physiologically capable of reproduction. Courtship and other breeding activity is not carried forward to culmination, however, because the external environmental factors needed to bring about breeding response are lacking. Thus, certain xerophilous species breed only when it rains, irrespective of day-length, and may skip a whole year when it does not. Rainfall and its effect appear to control the breeding of many tropical species. Among temperate zone species cold and comparatively sunless and foodless winter conditions may be far more important as inhibitors than mere shortness of day *under natural conditions*. Conversely, Sooty Terns on Ascension Island breed four times every three years in an equable oceanic island environment that apparently produces sufficient food to enable the survival of young at any season.

The migratory journey to the breeding grounds (e.g., that taken by charadriiform birds that "winter" on equatorial islands) may be timed in part by a genetically fixed rate of gonad recrudescence. When the gonads of both young and adults reach a certain developmental threshold they may be then, and then only, in a condition to respond to environmental influences that stimulate the exteroceptors and anterior pituitary. Thus would the gonads become even more active, leading to behavioural reactions between the sexes, until the birds reached a condition that caused them to depart for the place where they were bred. The same may occur in migrants that "winter" in temperate zones and may partly control the breeding seasons of the many tropical birds that do not ovulate during the monsoon. It is not yet known whether the anterior pituitary, too, has a refractory phase.

After the "spring" initiation of spermatogenesis, the sexual cycles of many species are modifiable from week to week by environmental events such as weather, food availability, and, finally, the presence of safe nesting sites. Each species has evolved its breeding response to a particular set of stimuli (including interactions between the sexes) and inhibitors. *No single over-all factor such as day-length or light-increment is responsible for the timing of avian breeding seasons. The breeding season is kept in step with the sun essentially by the external factors that permit nidification, ovulation and the survival of young on the habitual breeding ground. Of these, the most important may be a safe nesting site, mild weather, and an abundance of the food on which the young are traditionally fed.*

APPENDIX: A SIMPLIFIED TECHNIQUE FOR QUICK ROUTINE DEMONSTRATION OF INTERSTITIAL AND TUBULE LIPOIDS OF THE AVIAN GONAD

By "lipoids" are meant any of the chemically diverse fatty substances that colour with Sudan Black or Scharlach R. (Scarlet R; Sudan IV) after formalin fixation. Sudan Black was first used in cytology by Lison (1934) and its use has been recommended strongly by Baker (1944), who stresses its much greater efficacy (in comparison with Sudan III and Sudan IV) in colouring lipoids other than triglycerides. Scharlach R., which was introduced by Michaelis about fifty years ago, and Sudan Black both colour fats in a purely physical way by entering and dissolving in the lipoid globules where they are more soluble than they are in 70% alcohol or other similar vehicles. Thus they do not act in the manner of dyes, and partly because of this they show little tendency to alter the appearance of cells or their inclusions. Sudan Black is of incalculable value for detailed histochemical investigation of lipoids in that it "unmasks" certain lipoids that remain unrevealed by treatment with Sudan III or IV. But for the purpose of simple and inexpensive demonstration of the total lipoid content of the organ at different stages of its cycle the following method is recommended.

Fixation should be carried out if at all possible immediately after death, at most within two hours. Immerse the testis in formal-calcium (Baker, 1944). Commercial formalin diluted to about 5% HCHO is also adequate provided prolonged storage is not contemplated. Although formalin-penetration is fast, careful snipping, first, of the tunic of any organ more than 3 mm. in diameter is advisable. Fixation should be continued for 24 to 36 hours.

Next, the tissue should be washed in running water for at least four hours to make absolutely sure that all formalin has been removed. For most satisfactory results gelatine embedding for 24 hours at 37°C. is advised. After this the tissue and embedding medium should be chilled, *not* frozen, for a few minutes in a refrigerator. The gelatine can now be trimmed into a small block and hardened in formal-calcium (or formalin as above) for another 24 hours and washed for about 30 minutes. Then it can be cut on the freezing microtome at about 10μ.

Colouring procedure: 1. Stand sections for about 30 seconds in 70% alcohol. 2. Transfer for about three minutes to solution of Scharlach R. 3. Dip in 70% alcohol. 4. Dip in water. 5. Transfer for about three minutes to Ehrlich's haematoxylin. 6. Blue in tapwater. 7. Differentiate, if necessary, in 0.5 HCl in water. 8. Mount in Farrant's or similar medium. Slide-clips help flatten gelatine sections and express air bubbles on the hotplate.

Scharlach R. may be made up as follows: 70% alcohol, 50 mls., acetone, 50 mls., to which is added enough Scharlach R. to saturate. *Filter before use.*

The above technique, after a little practice, will bring lipoids into brilliant scarlet relief against the remaining familiar structures blued by Ehrlich's haematoxylin. The second testis, or a fragment of the first if one is damaged by shot, should be fixed in Bouin's, Flemming's, or any other good general-purpose fixative, wax-sectioned (the lipoids are now lost) and stained with Masson's trichrome or other routine method to reveal more clearly the spermatogenetic stages, Leydig cell-size and nuclear detail, and the postnuptial rehabilitation of the *tunica albuginea*. If fixation must be carried out in the field, formal-calcium or formalin is fairly satisfactory for the wax-section material as well.

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