THE FERTILIZATION AND EARLY DEVELOPMENT OF THE PIGEON'S EGG, A DISSERTATION, ZOOLOGY

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The fertilization and early development of the pigeon's egg, A Dissertation, Zoology by Eugene Howard Harper

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THE FERTILIZATION AND EARLY DEVELOPMENT OF THE PIGEON'S EGG

A DISSERTATION

SUBMITTED TO THE FACULTIES OF THE GRADUATE SCHOOLS OF ARTS, LITERATURE, AND SCIENCE, IN CANDIDACY FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

ZOOLOGY

BY
EUGENE HOWARD HARPER

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EUGENE HOWARD HARPER, PH. D.

WITH 4 DOUBLE PLATES AND 6 DIAGRAMS IN THE TEXT.

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The investigation, the results of which are here described, was proposed to me by Dr. C. O. Whitman, and the work has been carried on under his direction, being designed as part of a more general work upon the Natural History of Pigeons. My thanks are due to Prof. Whitman for his encouragement and suggestions and his assistance in obtaining the material.

In this paper the aim has been to get a view of that period of development of the bird's egg which has hitherto been scarcely touched upon, including the maturation, fertilization and early cleavage. Material was obtained from only one species, the common pigeon, Columba livia domestica. On account of the prolonged breeding season of pigeons and the ease with which they may be kept in confinement, they are

certainly better adapted to furnish material for studies of this sort than any other bird.

About the early development of the large meroblastic eggs comparatively little is known. This has remained true in spite of the thoroughness with which the embryonic stages of selachian and chick have been studied. As a result of the work of a number of investigators, chiefly Rückert, there is now a fairly complete general survey of the fertilization and early stages of the selachian egg. Observations upon the early development of the bird's egg are very few. Some of the early cleavage stages of the chick were figured by Coste, and Balfour contributed some observations. The internal phenomena of the egg during maturation, fertilization and early cleavage have remained an open field for investigation.

Upon the ovarian history of the bird's egg observations have been quite numerous. The paper of Holl, 90, upon the hen's egg may be mentioned as one of the most important.

The development of the large meroblastic eggs obviously presents numerous problems. In this paper the stages of the egg obtained are scattered over a considerable period, and present glimpses of various phases of maturation, fertilization and early cleavage. A few stages of the ovarian egg have also been introduced.

Methods.

The method followed has been to fix the whole egg before attempting to remove the germinal area. The oviduct is removed, the position of the egg being carefully noted, as this enables one to judge the approximate stage in development and determines the subsequent treatment in staining. The portion of the oviduct containing the egg is then cut off, immersed in the fixing fluid and slit open underneath the liquid. In case of an egg which is free in the body cavity, with some caution the body may be inverted over the fixing fluid, allowing the egg to drop out. The large ovarian egg may be fixed long enough to allow the fluid to penetrate the disc, then hardened in alcohol and the germinal area subsequently dissected out.

The choice of fixing fluids is somewhat limited, since many of them leave the disc too brittle to stand the subsequent treatment, and washing in water is undesirable. The picro-acetic mixtures have been chiefly used. Long fixation is not necessary or desirable, owing to the swelling of the yolk, which is apt to distort the disc.

It is well to cut out a considerable portion of the surrounding yolk with the disc and then to float this piece into a shallow watch-glass and

allow it to remain with the convex surface down in the watch-glass through the washing and hardening treatment. Lying on a flat surface tends to warp and often crack the disc. It should be trimmed evenly all around to overcome the tendency to curl in one direction. Occasionally the egg membrane will come off easily before or even after fixation. If not, the sharpness of the knife must be depended on to overcome this difficulty. Of course the knife should strike the inner side of the disc in its descent.

The abundance of the yolk and its obscuration of other structures would seem to make it desirable to use a stain which should mask the yolk as much as possible. In all but the fertilization stages the nuclei are surrounded by areas tolerably free from granules, and this is especially true of the sperm nuclei in their later divisons, which are surrounded by very large granule-free areas. For this reason the iron-alum hæmatoxylin stain is workable, and possesses besides an advantage in differentiating certain areas in the cytoplasm during its amœboid changes, which are less conspicuous with a stain which masks the yolk. The different degrees of extraction of the stain in the different areas of the cytoplasm is a highly desirable feature.

Some Observations on the Breeding Habits of the Common Pigeon.

The fact that the pigeon breeds so readily in confinement makes possible a close observation of its breeding habits. As is well known, the special instincts displayed in connection with reproduction are more highly developed in the pigeon than in the common fowl. These complex instincts are associated with monogamy, which reaches a type of development in the pigeon which is very high among birds. For example, the feeding of the young with "pigeon milk" may be mentioned. It is only with the earlier manifestations of the reproductive instincts prior to egg-laying that we are here concerned.

It might be supposed that in the case of a domesticated bird breeding readily in confinement, such as the pigeon, some approach might be made toward an exact method for determining the time of fertilization of the egg. The time of egg-laying is approximately definite, as all breeders know. The common pigeon ordinarily lays two eggs at a sitting, occasionally only one. The first egg is regularly laid late in the afternoon. The second egg will be laid early in the afternoon of the second day following.

It is evident that the determination of the time of fertilization of the second egg of the pair and the length of time taken in its passage

through the oviduct would be a simpler matter than to determine from external signs when the first egg is fertilized. It has been found that after the first egg is laid, in the course of a very few hours the second egg becomes detached from the ovary, is fertilized, and passes into the oviduct.

As stated above, the first egg is laid late in the afternoon. Early in the evening the second egg becomes free from its capsule in the ovary and enters the oviduct. In all cases observed this has taken place between seven and nine o'clock. The time taken in passing down the oviduct is relatively short, the far larger part of the time which elapses before the egg is laid being spent in the lower portion, known as the uterus, or shell-gland. It is evident that the second egg of a pair may be obtained at approximately any stage desired, beginning with a period a few hours before its fertilization.

The question arises whether there may be any criteria found for judging the time of fertilization of the first egg. It might be thought from analogy with the mammalia that the time of copulation would furnish such a criterion. It is quite plain from the regularity of the history of the second egg, as given above, that the exact period when the egg is freed from its capsule is dependent upon the female organization, and would be likely to occur at some definite period, probably at night. A moment's thought would, however, make it plain that it is highly improbable that a periodical receptivity, or period of heat, should be displayed by the female at this time. Experience of the writer has shown that any violent movement of the animal at this time is likely to result in a broken egg. Of course, such an egg as the bird's cannot be retained in the oviduct to await fertilization. Sperms are stored in advance, and the critical passage of the egg, after leaving its tough capsule in the ovary, through the oviduct till it acquires its coating of albumen and a shell, occurs at night when there are no movements of the animal to endanger its safety. The period of receptivity of the female is prior to this series of events. Copulation is repeated so often that no definiteness could be attached to it as a criterion. The question then arises whether the period of receptivity of the female has any definite duration, so as to indicate in this way when the maturation of the egg is taking place. From analogy with the mammal and with many birds, such as the common fowl, we commonly think of ovulation as exclusively a female function, going on regardless of whether the eggs produced are fertilized or not. Thus the common fowl produces unfertilized eggs regularly in the absence of a male. In the pigeon, however, ovulation is delayed until mating. When a mature pair ready

for mating are put together, egg-laying ordinarily ensues at the end of a rather definite period, at the least eight days. The female functions are held in abeyance till the proper stimulus is received from a mate. The maturing of the egg is so exclusively a female function that it seems odd at first thought that an apparent exception should occur to the rule. Of course, we know that the final maturation of the egg, or the giving off of the polar bodies, awaits in most animals the act of fertilization. But here the effect is produced upon the egg by the entrance of sperms. How mating itself and the act of copulation could influence the ripening of the egg in the ovary is another problem. In this connection the curious fact must be mentioned that two female pigeons placed in confinement together may both take to laying eggs. The function of ovulation is in a state of tension, so to speak, that requires only a slight stimulus, "mental" apparently in this case, to set the mechanism to working. At any rate, it is impossible to regard the presence of sperm in the oviduct as an essential element of the stimulus to ovulation, although it may have an important influence in the normal case. Our attention is directed to the various and complex instincts of the male which come under the head of courtship, both before and after mating is effected, as furnishing a part of the stimulus to the female reproductive organs.

Phylogenetic considerations would lead us to consider the peculiar habits of the pigeon as recently acquired. The retention of ova in the unmated female, is in particular not very firmly fixed, as the facts stated show. The habits of the common fowl are certainly more primitive. In monogamous birds it might be expected that the function of ovulation would be adjusted so as to take place only after mating, inasmuch as it is probable that in a state of nature mating may be delayed for various causes, and the production of an unfertilized egg is no trifling loss, as in the mammal. In polygamous birds mating is sure to occur, and the female functions may be adjusted for continuous ovulation, with the practical certainty that in nature no unfertilized egg will be produced.

The complex reproductive instincts of the pigeon, displayed in their highest form in the male, are matters of common observation among those who have observed pigeons, and need not be dwelt upon at great length.

As is well known, the strutting of male pigeons is not simply a feature of courtship and rivalry among males. It is continued until egg-laying begins, and is accompanied by a less active similar manifestation by the female. It is in fact an accompaniment of the whole period