THE REPRODUCTIVE BEHAVIOR OF RING DOVES

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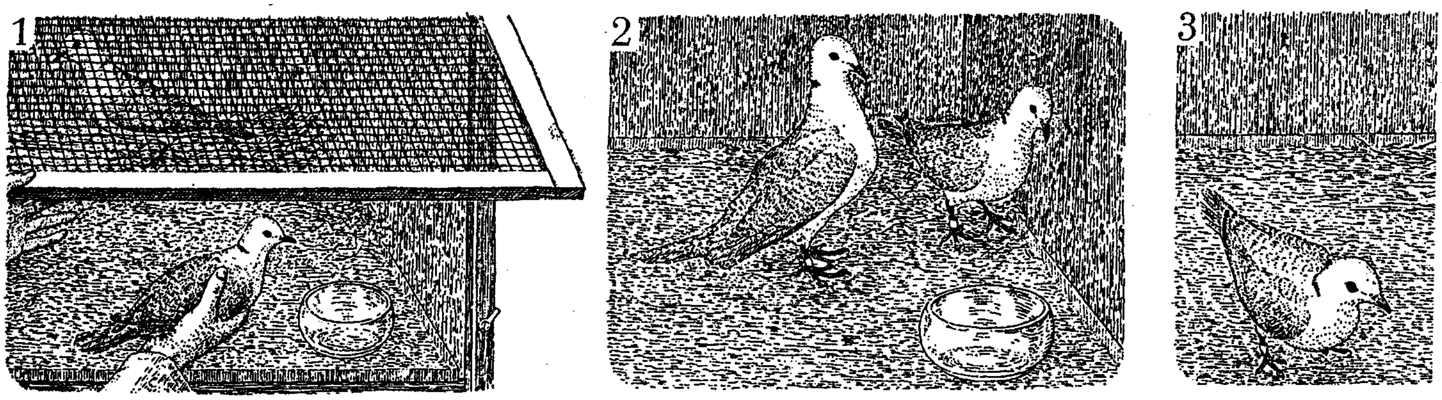
The Reproductive Behavior of Ring Doves

An account of experiments showing that the changes in activity that constitute the behavior cycle are governed by interactions of outside stimuli, the hormones and the behavior of each mate

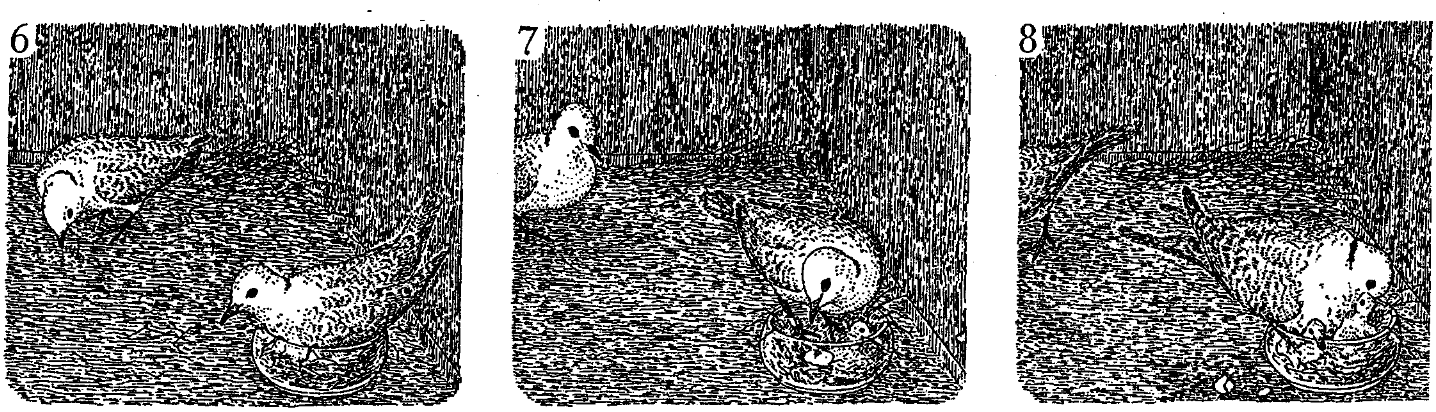
by Daniel S. Lehrman

In recent years the study of animal behavior has proceeded along two different lines, with two groups of investigators formulating problems in different ways and indeed approaching the problems from different points of view. The comparative psychologist traditionally tends first to ask a question and then to attack it by way of animal experimentation. The ethologist, on the other hand, usually begins by observing the normal activity of an animal and then seeks to identify and analyze specific behavior patterns characteristic of the species.

The two attitudes can be combined. The psychologist can begin, like the ethologist, by watching an animal do what it does naturally, and only then ask questions that flow from his observations. He can go on to manipulate experimental conditions in an effort to discover the psychological and biological events that give rise to the behavior under study and perhaps to that of other animals as well. At the Institute of Animal Behavior at Rutgers University we have taken this approach to study in detail the reproductive-behavior cycle of the ring dove (*Streptopelia risoria*). The highly specific changes in behavior that occur in the course of the cycle, we find, are governed by complex psycho-



REPRODUCTIVE-BEHAVIOR CYCLE begins soon after a male and a female ring dove are introduced into a cage containing nesting material (hay in this case) and an empty glass nest bowl (*1*). Courtship activity, on the first day, is characterized by the "bowing

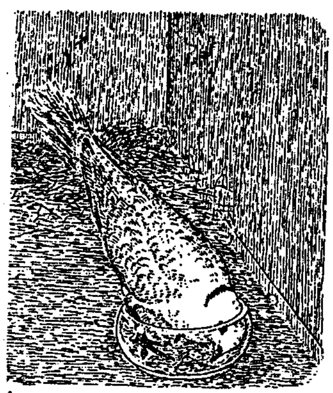


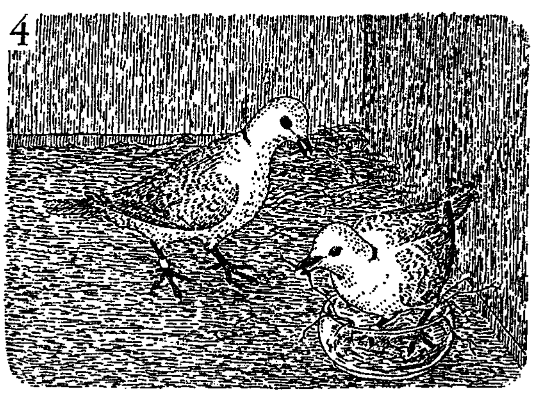
CYCLE CONTINUES as the adult birds take turns incubating the eggs (*6*), which hatch after about 14 days (*7*). The newly hatched squabs are fed "crop-milk," a liquid secreted in the gullets of the adults (*8*). The parents continue to feed them, albeit reluctantly, biological interactions of the birds' inner and outer environments.

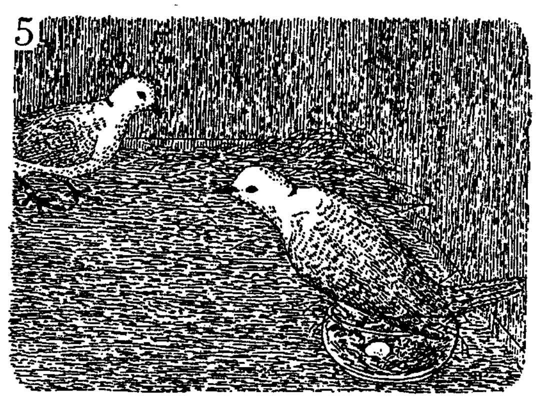
The ring dove, a small relative of the domestic pigeon, has a light gray back, creamy underparts and a black semicircle (the "ring") around the back of its neck. The male and female look alike and can only be distinguished by surgical exploration. If we place a male and a female ring dove with previous breeding experience in a cage containing an empty glass bowl and a supply of nesting material, the birds invariably enter on their normal behavioral cycle, which follows a predictable course and a fairly regular time schedule. During the first day the principal activity is courtship: the male struts around, bowing and cooing at the female. After several hours the birds announce their selection of a nest site (which in nature would be a concave place and in our cages is the glass bowl) by crouching in it and uttering a distinctive coo. Both birds participate in building the nest, the male usually gathering material and carrying it to the female, who stands in the bowl and constructs the nest. After a week or more of nest-building, in the course of which the birds copulate, the female becomes noticeably more attached to the nest and difficult to dislodge; if one attempts to lift her off the nest, she may grasp it with her claws and take it along. This behavior usually indicates that the female is about to lay her eggs. Between seven and 11 days after the beginning of the courtship she produces her first egg, usually at about five o'clock in the afternoon. The female dove sits on the egg and then lays a second one, usually at about nine o'clock in the morning two days later. Sometime that day the male takes a turn sitting; thereafter the two birds alternate, the male sitting for about six hours in the middle of each day, the female for the remaining 18 hours a day.

In about 14 days the eggs hatch and the parents begin to feed their young "crop-milk," a liquid secreted at this stage of the cycle by the lining of the adult dove's crop, a pouch in the bird's gullet. When they are 10 or 12 days old, the squabs leave the cage, but they continue to beg for and to receive food from the parents. This continues until the squabs are about two weeks old, when the parents become less and less willing to feed them as the young birds gradually develop the ability to peck for grain on the floor of the cage. When the young are about 15 to 25 days old, the adult male begins once again to bow and coo; nest-building is resumed, a new clutch of eggs is laid and the cycle is repeated. The entire cycle lasts about six or seven weeks and—at least in our laboratory, where it is always spring because of controlled light and temperature conditions—it can continue throughout the year.

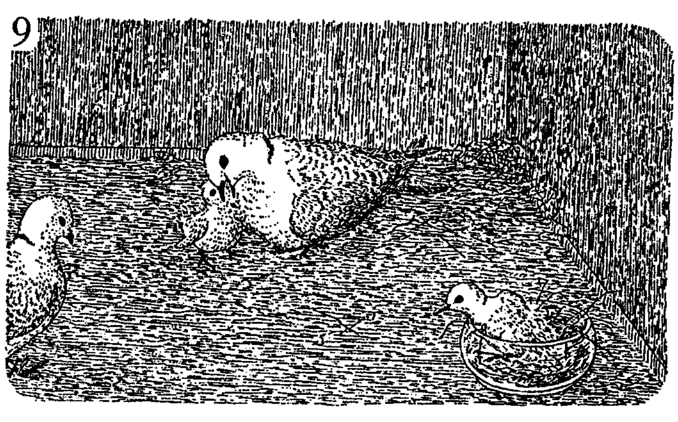
The variations in behavior that constitute the cycle are not merely casual or superficial changes in the birds' preoccupations; they represent striking changes in the overall pattern of activity and in the atmosphere of the breeding cage. At its appropriate stage each of the kinds of behavior I have described represents the predominant activity of the animals at the time. Furthermore, these changes in behavior are not just responses to changes in the external situation. The birds do not build the nest merely because the nesting material is available; even if nesting material is in the cage throughout the cycle, nest-building behavior is concentrated,

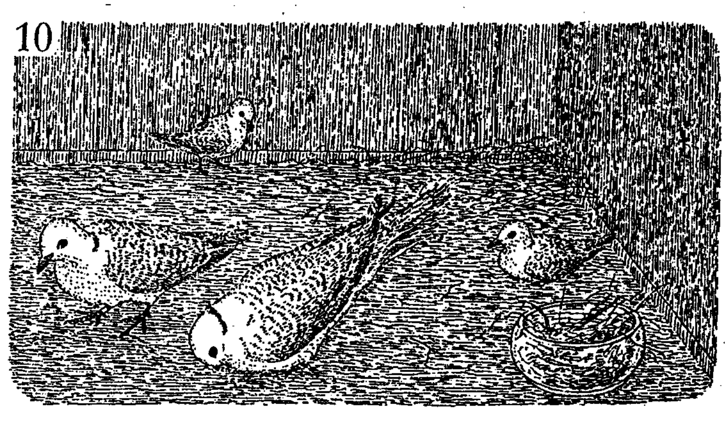






coo" of the male (*2*). The male and then the female utter a distinctive "nest call" to indicate their selection of a nesting site (*3*). **There follows a week or more of cooperation in nest-building (*4*), culminating in the laying of two eggs at precise times of day (*5*).**





as the young birds learn to peck for grain themselves (*9*). When the squabs are between two and three weeks old, the adults ignore them and start to court once again, and a new cycle begins (*10*). **Physical changes during the cycle are shown on the next page.**

as described, at one stage. Similarly, the birds react to the eggs and to the young only at appropriate stages in the cycle.

These cyclic changes in behavior therefore represent, at least in part, changes in the internal condition of the animals rather than merely changes in their external situation. Furthermore, the changes in behavior are associated with equally striking and equally pervasive changes in the anatomy and the physiological state of the birds. For example, when the female dove is first introduced into the cage, her oviduct weighs some 800 milligrams. Eight or nine days later, when she lays her first egg, the oviduct may weigh 4,000 milligrams. The crops of both the male and the female weigh some 900 milligrams when the birds are placed in the cage, and when they start to sit on the eggs some 10 days later they still weigh about the same. But two weeks afterward, when the eggs hatch, the parents' crops may weigh as much as 3,000 milligrams. Equally striking changes in the condition of the ovary, the weight of the testes, the length of the gut, the weight of the liver, the microscopic structure of the pituitary gland and other physiological indices are correlated with the behavioral cycle.

Now, if a male or a female dove is placed alone in a cage with nesting material, no such cycle of behavioral or anatomical changes takes place. Far from producing two eggs every six or seven weeks, a female alone in a cage lays no eggs at all. A male alone shows no interest when we offer it nesting material, eggs or young. The cycle of psychobiological changes I have described is, then, one that occurs more or less synchronously in each member of a pair of doves living together but that will not occur independently in either of the pair living alone.

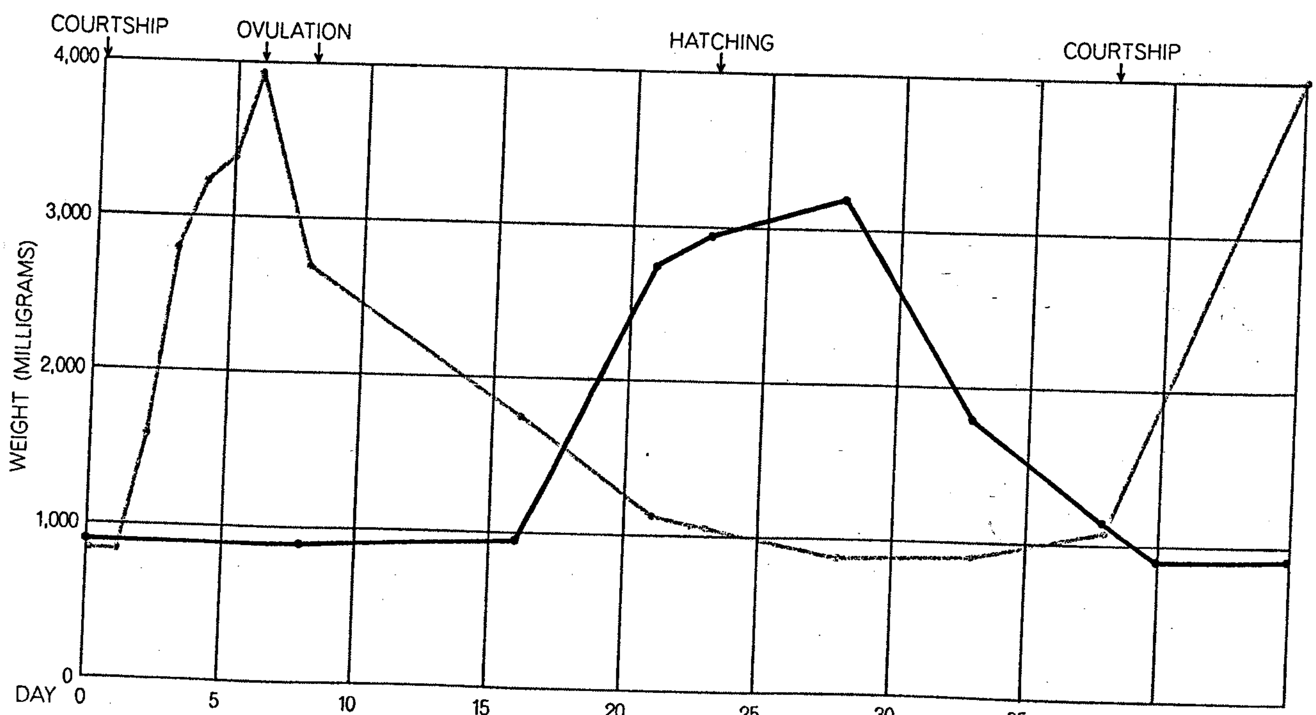
In a normal breeding cycle both the male and the female sit on the eggs almost immediately after they are laid. The first question we asked ourselves was whether this is because the birds are always ready to sit on eggs or because they come into some special condition of readiness to incubate at about the time the eggs are produced.

We kept male and female doves in isolation for several weeks and then placed male-female pairs in test cages, each supplied with a nest bowl containing a normal dove nest with two eggs. The birds did not sit; they acted almost as if the eggs were not there. They courted, then built their own nest (usually on top of the planted nest and its eggs, which we had to keep fishing out to keep the stimulus situation constant!), then finally sat on the eggs—five to seven days after they had first encountered each other.

This clearly indicated that the doves are not always ready to sit on eggs; under the experimental conditions they changed from birds that did not want to incubate to birds that did want to incubate in five to seven days. What had induced this change? It could not have been merely the passage of time since their last breeding experience, because this had varied from four to six or more weeks in different pairs, whereas the variation in time spent in the test cage before sitting was only a couple of days.

Could the delay of five to seven days represent the time required for the birds to get over the stress of being handled and become accustomed to the strange cage? To test this possibility we placed pairs of doves in cages without any nest bowls or nesting material and separated each male and female by an opaque partition. After seven days we removed the partition and introduced nesting material and a formed nest with eggs. If the birds had merely needed time to recover from being handled and become acclimated to the cage, they should now have sat on the eggs immediately. They did not do so; they sat only after five to seven days, just as if they had been introduced into the cage only when the opaque partition was removed.

The next possibility we considered was that in this artificial situation stimulation from the eggs might induce the change from a nonsitting to a sitting "mood" but that this effect required five to seven days to reach a threshold value at which the behavior would change.



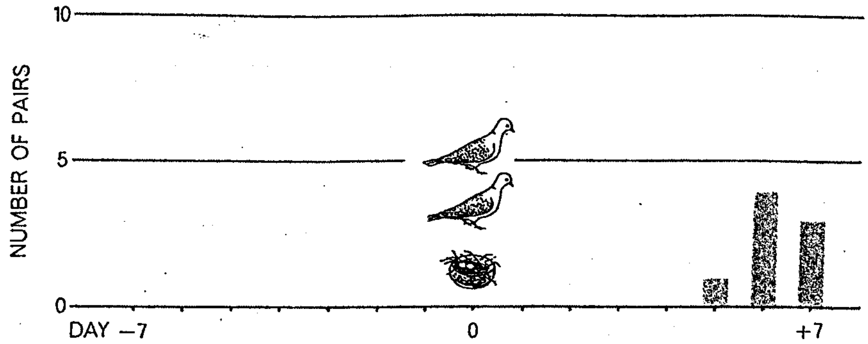
ANATOMICAL AND PHYSIOLOGICAL changes are associated with the behavioral changes of the cycle. The chart gives average weights of the crop (*black curve*) and the female oviduct (*color*) at various stages measured in days after the beginning of courtship.

We therefore placed pairs of birds in test cages with empty nest bowls and a supply of nesting material but no eggs. The birds courted and built nests. After seven days we removed the nest bowl and its nest and replaced it with a fresh bowl containing a nest and eggs. All these birds sat within two hours.

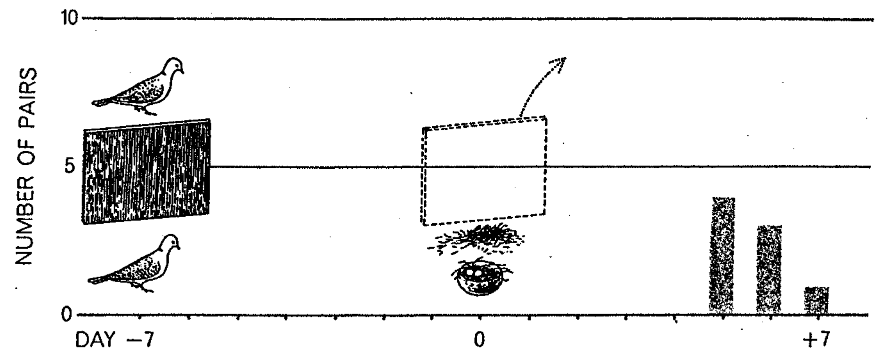
It was now apparent that some combination of influences arising from the presence of the mate and the availability of the nest bowl and nesting material induced the change from nonreadiness to incubate to readiness. In order to distinguish between these influences we put a new group of pairs of doves in test cages without any nest bowl or nesting material. When, seven days later, we offered these birds nesting material and nests with eggs, most of them did not sit immediately. Nor did they wait the full five to seven days to do so; they sat after one day, during which they engaged in intensive nest-building. A final group, placed singly in cages with nests and eggs, failed to incubate at all, even after weeks in the cages.

In summary, the doves do not build nests as soon as they are introduced into a cage containing nesting material, but they will do so immediately if the nesting material is introduced for the first time after they have spent a while together; they will not sit immediately on eggs offered after the birds have been in a bare cage together for some days, but they will do so if they were able to do some nest-building during the end of their period together. From these experiments it is apparent that there are two kinds of change induced in these birds: first, they are changed from birds primarily interested in courtship to birds primarily interested in nest-building, and this change is brought about by stimulation arising from association with a mate; second, under these conditions they are further changed from birds primarily interested in nest-building to birds interested in sitting on eggs, and this change is encouraged by participation in nest-building.

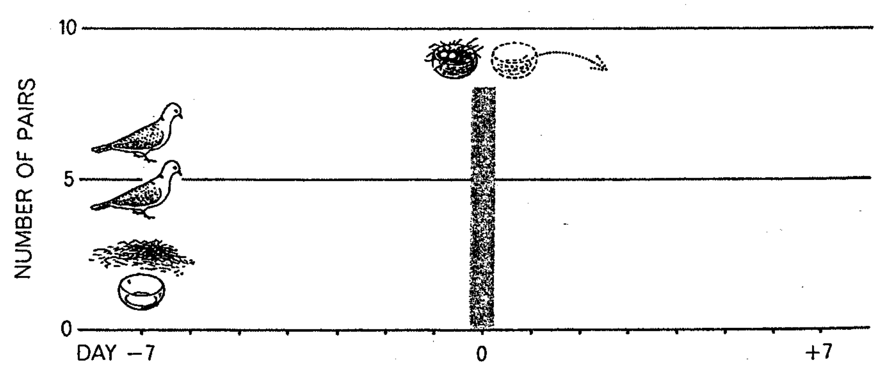
The course of development of readiness to incubate is shown graphically by the results of another experiment, which Philip N. Brody, Rochelle Wortis and I undertook shortly after the ones just described. We placed pairs of birds in test cages for varying numbers of days, in some cases with and in others without a nest bowl and nesting material. Then we introduced a nest and eggs into the cage. If neither bird sat within three hours, the test was scored as nega-



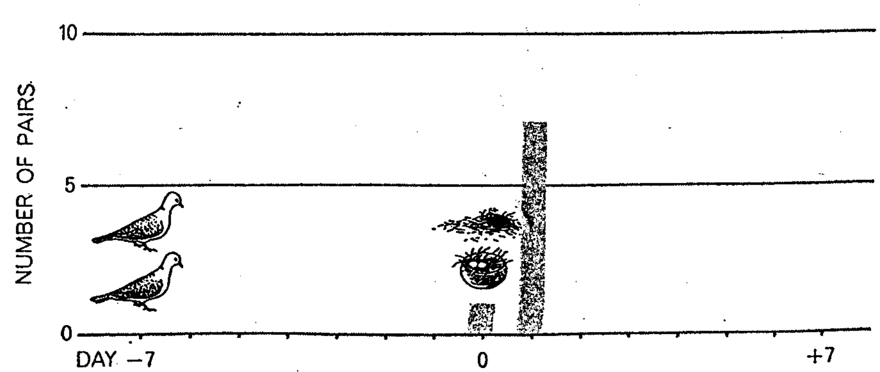
READINESS TO INCUBATE was tested with four groups of eight pairs of doves. Birds of the first group were placed in a cage containing a nest and eggs. They went through courtship and nest-building behavior before finally sitting after between five and seven days.



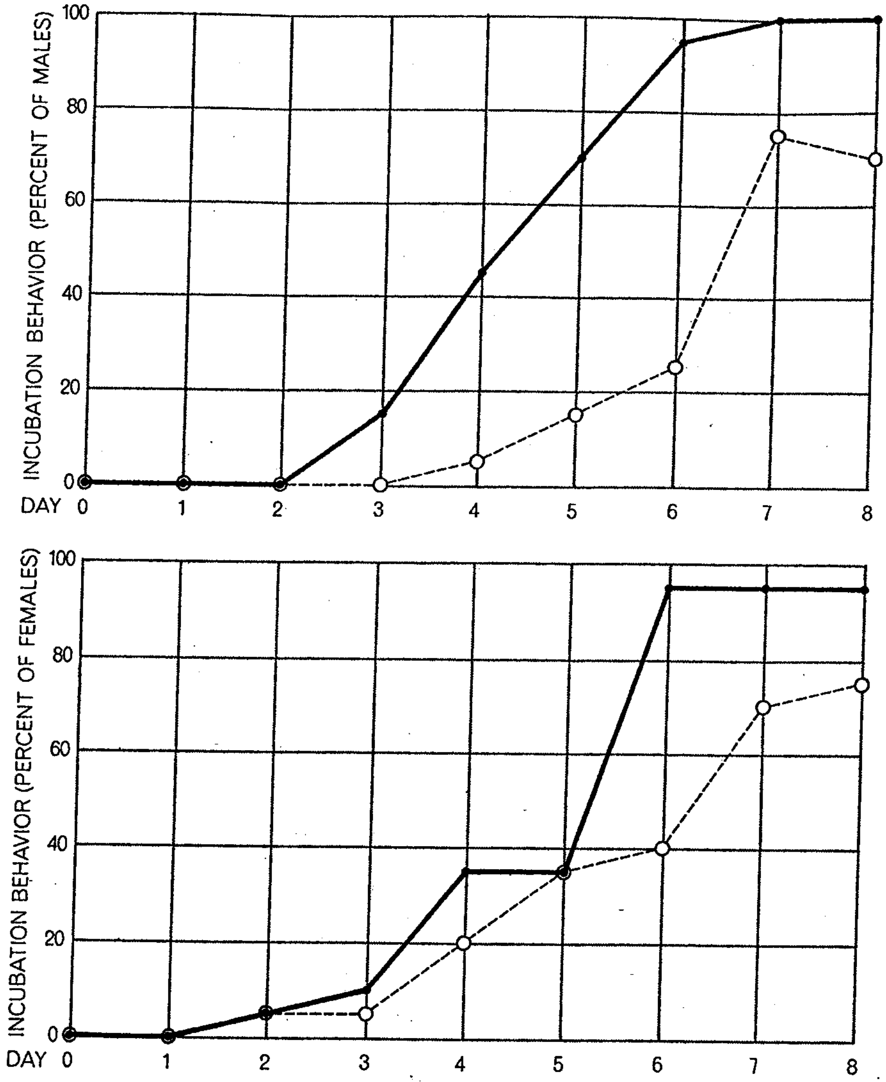
EFFECT OF HABITUATION was tested by keeping two birds separated for seven days in the cage before introducing nest and eggs. They still sat only after five to seven days.



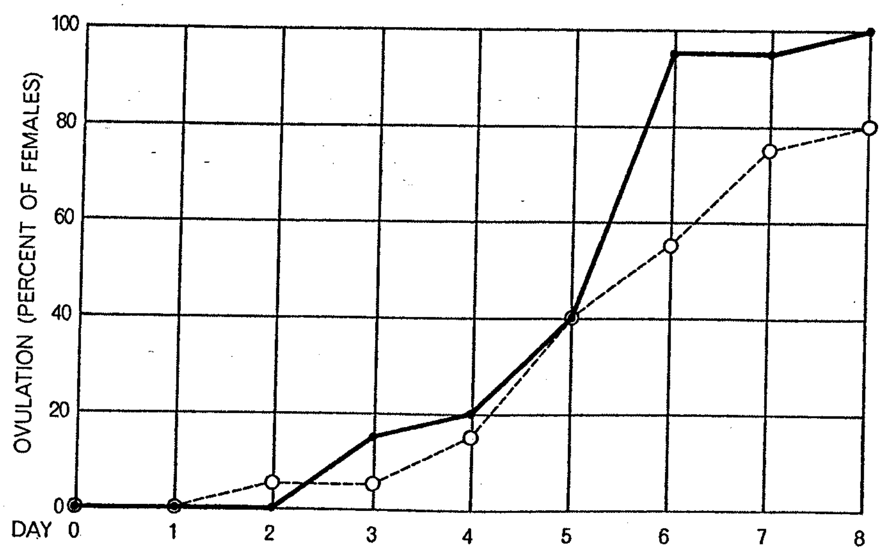
MATE AND NESTING MATERIAL had a dramatic effect on incubation-readiness. Pairs that had spent seven days in courtship and nest-building sat as soon as eggs were offered.



PRESENCE OF MATE without nesting activity had less effect. Birds that spent a week in cages with no nest bowls or hay took a day to sit after nests with eggs were introduced.



DURATION OF ASSOCIATION with mate and nesting material affects incubation behavior. The abscissas give the length of the association for different groups of birds. The plotted points show what percentage of each group sat within three hours of being offered eggs. The percentage increases for males (*top*) and females (*bottom*) as a function of time previously spent with mate (*open circles*) or with mate and nesting material (*solid dots*).



OVULATION is similarly affected. These curves, coinciding closely with those of the bottom chart above, show the occurrence of ovulation in the same birds represented there.

tive and both birds were removed for autopsy. If either bird sat within three hours, that bird was removed and the other bird was given an additional three hours to sit. The experiment therefore tested—independently for the male and the female—the development of readiness to incubate as a function of the number of days spent with the mate, with or without the opportunity to build a nest.

It is apparent [*see top illustration at left*] that association with the mate gradually brings the birds into a condition of readiness to incubate and that this effect is greatly enhanced by the presence of nesting material. Exposure to the nesting situation does not stimulate the onset of readiness to incubate in an all-or-nothing way; rather, its effect is additive with the effect of stimulation provided by the mate. Other experiments show, moreover, that the stimulation from the mate and nesting material is sustained. If either is removed, the incidence of incubation behavior decreases.

The experiments described so far made it clear that external stimuli normally associated with the breeding situation play an important role in inducing a state of readiness to incubate. We next asked what this state consists of physiologically. As a first approach to this problem we attempted to induce incubation behavior by injecting hormones into the birds instead of by manipulating the external stimulation. We treated birds just as we had in the first experiment but injected some of the birds with hormones while they were in isolation, starting one week before they were due to be placed in pairs in the test cages. When both members of the pair had been injected with the ovarian hormone progesterone, more than 90 percent of the eggs were covered by one of the birds within three hours after their introduction into the cage instead of five to seven days later. When the injected substance was another ovarian hormone—estrogen—the effect on most birds was to make them incubate after a latent period of one to three days, during which they engaged in nest-building behavior. The male hormone testosterone had no effect on incubation behavior.

During the 14 days when the doves are sitting on the eggs, their crops increase enormously in weight. Crop growth is a reliable indicator of the secretion of the hormone prolactin by the birds' pituitary glands. Since this growth coincides with the development of incubation behavior and culminates in the secretion of the crop-milk the birds feed to their young after the eggs hatch, Brody and I have recently examined the effect of injected prolactin on incubation behavior. We find that prolactin is not so effective as progesterone in inducing incubation behavior, even at dosage levels that induce full development of the crop. For example, a total prolactin dose of 400 international units induced only 40 percent of the birds to sit on eggs early, even though their average crop weight was about 3,000 milligrams, or more than three times the normal weight. Injection of 10 units of the hormone induced significant increases in crop weight (to 1,200 milligrams) but no increase in the frequency of incubation behavior. These results, together with the fact that in a normal breeding cycle the crop begins to increase in weight only after incubation begins, make it unlikely that prolactin plays an important role in the initiation of normal incubation behavior in this species. It does, however, seem to help to maintain such behavior until the eggs hatch.

Prolactin is much more effective in inducing ring doves to show regurgitation-feeding responses to squabs. When 12 adult doves with previous breeding experience were each injected with 450 units of prolactin over a seven-day period and placed, one bird at a time, in cages with squabs, 10 of the 12 fed the squabs from their engorged crops, whereas none of 12 uninjected controls did so or even made any parental approaches to the squabs.

This experiment showed that prolactin, which is normally present in considerable quantities in the parents when the eggs hatch, does contribute to the doves' ability to show parental feeding behavior. I originally interpreted it to mean that the prolactin-induced engorgement of the crop was necessary in order for any regurgitation feeding to take place, but E. Klinghammer and E. H. Hess of the University of Chicago have correctly pointed out that this was an error, that ring doves are capable of feeding young if presented with them rather early in the incubation period. They do so even though they have no crop-milk, feeding a mixture of regurgitated seeds and a liquid. We are now studying the question of how early the birds can do this and how this ability is related to the onset of prolactin secretion.

The work with gonad-stimulating hormones and prolactin demonstrates that the various hormones successively produced by the birds' glands during their reproductive cycle are capable of inducing the successive behavioral changes that characterize the cycle.

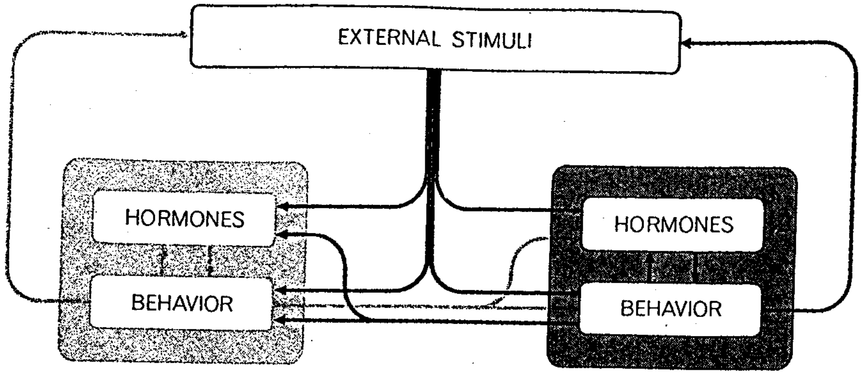
Up to this point I have described two main groups of experiments. One group demonstrates that external stimuli induce changes in behavioral status of a kind normally associated with the progress of the reproductive cycle; the second shows that these behavioral changes can also be induced by hormone administration, provided that the choice of hormones is guided by knowledge of the succession of hormone secretions during a normal reproductive cycle. An obvious—and challenging—implication of these results is that external stimuli may induce changes in hormone secretion, and that environment-induced hormone secretion may constitute an integral part of the mechanism of the reproductive behavior cycle. We have attacked the problem of the environmental stimulation of hormone secretion in a series of experiments in which, in addition to examining the effects of external stimuli on the birds' behavioral status, we have examined their effects on well-established anatomical indicators of the presence of various hormones.

Background for this work was provided by two classic experiments with the domestic pigeon, published during the 1930's, which we have verified in the ring dove. At the London Zoo, L. H. Matthews found that a female pigeon would lay eggs as a result of being placed in a cage with a male from whom she was separated by a glass plate. This was an unequivocal demonstration that visual and/or auditory stimulation provided by the male induces ovarian development in the female. (Birds are quite insensitive to olfactory stimulation.) And M. D. Patel of the University of Wisconsin found that the crops of breeding pigeons, which develop strikingly during the incubation period, would regress to their resting state if the incubating birds were removed from their nests and would fail to develop at all if the birds were removed before crop growth had begun. If, however, a male pigeon, after being removed from his nest, was placed in an adjacent cage from which he could see his mate still sitting on the eggs, his crop would develop just as if he were himself incubating! Clearly stimuli arising from participation in incubation, including visual stimuli, cause the doves' pituitary glands to secrete prolactin.

Our autopsies showed that the incidence of ovulation in females that had associated with males for various periods coincided closely with the incidence of incubation behavior [*see bottom illustration on opposite page*]; statistical analysis reveals a very high degree of association. The process by which the dove's ovary develops to the point of ovulation includes a period of estrogen secretion followed by one of progesterone secretion, both induced by appropriate ovary-stimulating hormones from the pituitary gland. We therefore conclude that stimuli provided by the male, augmented by the presence of the nest bowl and nesting material, induce the secretion of gonad-stimulating hormones by the female's pituitary, and that the onset of readiness to incubate is a result of this process.

As I have indicated, ovarian development, culminating in ovulation and egg-laying, can be induced in a female dove merely as a result of her seeing a male through a glass plate. Is this the result of the mere presence of another bird or of something the male does because he is a male? Carl Erickson and I have begun to deal with this question. We placed 40 female doves in separate cages, each separated from a male by a glass plate. Twenty of the stimulus animals were normal, intact males, whereas the remaining 20 had been castrated several weeks before. The intact males all exhibited vigorous bow-cooing immediately on being placed in the cage, whereas none of the castrates did so. Thirteen of the 20 females with intact males ovulated during the next seven days, whereas only two of those with the castrates did so. Clearly ovarian development in the female is not induced merely by seeing another bird but by seeing or hearing it act like a male as the result of the effects of its own male hormone on its nervous system.

Although crop growth, which begins early in the incubation period, is apparently stimulated by participation in incubation, the crop continues to be large and actively secreting for quite some time after the hatching of the eggs. This suggests that stimuli provided by the squabs may also stimulate prolactin secretion. In our laboratory Ernst Hansen substituted three-day-old squabs for eggs in various stages of incubation and after four days compared the adults' crop weights with those of birds that had continued to sit on their eggs dur-



INTERACTIONS that appear to govern the reproductive-behavior cycle are suggested here. Hormones regulate behavior and are themselves affected by behavioral and other stimuli. And the behavior of each bird affects the hormones and the behavior of its mate.

ing the four days. He found that the crops grow even faster when squabs are in the nest than when the adults are under the influence of the eggs; the presence of squabs can stimulate a dove's pituitary glands to secrete more prolactin even before the stage in the cycle when the squabs normally appear.

This does not mean, however, that any of the stimuli we have used can induce hormone secretion at *any* time, regardless of the bird's physiological condition. If we place a pair of ring doves in a cage and allow them to go through the normal cycle until they have been sitting on eggs for, say, six days and we then place a glass partition in the cage to separate the male from the female and the nest, the female will continue to sit on the eggs and the male's crop will continue to develop just as if he were himself incubating. This is a simple replication of one of Patel's experiments. Miriam Friedman and I have found, however, that if the male and female are separated from the beginning, so that the female must build the nest by herself and sit alone from the beginning, the crop of the male does not grow. By inserting the glass plate at various times during the cycle in different groups of birds, we have found that the crop of the male develops fully only if he is not separated from the female until 72 hours or more after the second egg is laid. This means that the sight of the female incubating induces prolactin secretion in the male only if he is in the physiological condition to which participation in nest-building brings him. External stimuli associated with the breeding situation do indeed induce changes in hormone secretion.

The experiments summarized here point to the conclusion that changes in the activity of the endocrine system are induced or facilitated by stimuli coming from various aspects of the environment at different stages of the breeding cycle, and that these changes in hormone secretion induce changes in behavior that may themselves be a source of further stimulation.

The regulation of the reproductive cycle of the ring dove appears to depend, at least in part, on a double set of reciprocal interrelations. First, there is an interaction of the effects of hormones on behavior and the effects of external stimuli—including those that arise from the behavior of the animal and its mate—on the secretion of hormones. Second, there is a complicated reciprocal relation between the effects of the presence and behavior of one mate on the endocrine system of the other and the effects of the presence and behavior of the second bird (including those aspects of its behavior induced by these endocrine effects) back on the endocrine system of the first. The occurrence in each member of the pair of a cycle found in neither bird in isolation, and the synchronization of the cycles in the two mates, can now readily be understood as consequences of this interaction of the inner and outer environments.

The physiological explanation of these phenomena lies partly in the fact that the activity of the pituitary gland, which secretes prolactin and the gonad-stimulating hormones, is largely controlled by the nervous system through the hypothalamus. The precise neural mechanisms for any complex response are still deeply mysterious, but physiological knowledge of the brain-pituitary link is sufficiently detailed and definite so that the occurrence of a specific hormonal response to a specific external stimulus is at least no more mysterious than any other stimulus-response relation. We are currently exploring these responses in more detail, seeking to learn, among other things, the precise sites at which the various hormones act. And we have begun to investigate another aspect of the problem: the effect of previous experience on a bird's reproductive behavior and the interactions between these experiential influences and the hormonal effects.

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