Extraretinal Photocontrol of Oviposition in Pinealectomized Domestic Fowl[1] (34171)

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Entrainment of oviposition cycles in domestic birds by the daily light-dark cycle is well established. In a 12- or 14-hr daily photoperiod, chickens lay most of their eggs in the early part of the light period, whereas Coturnix quail lay most of their eggs during the latter part of the light period (1–4). Reversal of the light–dark cycle caused a shift in the time of oviposition to the new photoperiod within 4–5 days. Following a change from a daily light–dark cycle to continuous light, the time of egg laying became uniformly distributed throughout the 24-hr period (1, 2). The transition of light to dark appears to initiate the daily oviposition cycle in chickens (1, 3, 5). A minimum of 2.5 hr of dark was reported to be adequate to alter time of oviposition (6).

The mechanism underlying light–dark cycle entrainment of oviposition remains uncertain. In both chickens and Coturnix quail, hypophysectomy 4–6 hr prior to an expected ovulation time prevented the expected ovulation (7, 8). Along with pituitary involvement, activity, wakefulness, and feeding pattern are reported to affect time of oviposition (1, 2). Light influence on ovulation and oviposition acting through the retina has been postulated (5), and the importance of the ocular region for light stimulation of testicular development in sparrows has been demonstrated (9). However, light stimulation of gonad development was reported in enucleated ducks (10). More recent research has revealed light–dark fluctuations of pineal enzyme level, in enucleated and ganglionectomized chickens (11). This work suggests that the pineal may be acting as an extraretinal receptor of light.

The close relationship between pineal and gonadal function (12–15) and the daily light–dark response in pineal enzyme metabolism (11, 16, 17) suggest the possibility that the influence of the daily light–dark cycle on oviposition in the fowl may be related to pineal function. The pineal involvement in free-running activity patterns of sparrows (18) could also relate to a pineal involvement in free-running oviposition time. This experiment was designed to test these hypotheses.

Materials and Methods. Forty-six white leghorn pullets, maintained in individual cages, were evenly divided into separate controlled environmental chambers. No outside or between chamber sound could be detected above the continuous background noise of ventilation and heater and cooler fans. Each cage in both chambers was equipped with a micro-smitch connected to a 20-channel event recorder. The micro-switches were activated by an egg passing over a trip lever which immediately reset after the egg passed. Oviposition time from 10 birds in each chamber (8 pinealectomized, 2 nonpinealectomized) was continuously and simultaneously recorded.

All of the birds in one chamber were enucleated and all except four were pinealectomized. In the remaining chamber the eyes were intact and all except four were pinealectomized. Pinealectomies were performed at 5–35 days of age. The birds were enucleated between 27 and 28 weeks of age. Pineals were surgically removed with jeweler forceps under a dissecting microscope. Partial or incomplete pinealectomies were microscopically determined at the termination of the experi-

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ment. Enucleation was accomplished by anesthetizing the bird, cutting the optic nerve, removing the intact eye and suturing the upper and lower lids together. Eight weeks were allowed for recovery and to determine if the birds would continue in egg production.

The lighting treatments consisted of an initial 12 hr of incandescent light and 12 hr of darkness/day. After recording the oviposition of the initial photoperiod, the light–dark cycle was reversed. To determine oviposition pattern response to photoperiod changes less than an absolute reversal, photoperiod was shifted by 6, 1, and 5 hrs, respectively. Following the first sequence fo reversal of light–dark cycle and lesser shifts in photoperiod, the lighting treatment was again reversed. However, in the second light reversal, aluminum plates were placed over the orbits in the enucleated birds and the entire head, with the exception of the comb, was covered with black tape. After the second light-dark reversal the birds were exposed to continuous light to determine free-running circadian pattern of oviposition.

Results and Discussion. Reversal of light–dark cycle caused a subsequent reversal in oviposition time in all treatment groups (Fig. 1). Prior to reversal of the photoperiod a small percentage of the eggs were laid in the dark. However, most of the ovipositions in the dark occurred just prior to the dark–light transition. Following the reversal

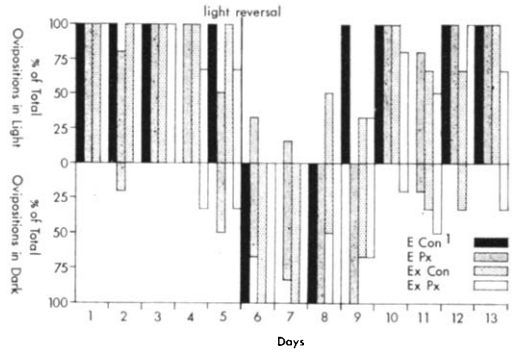

FIG. 1. Oviposition time before and after reversal of 12-hr light and 12-hr dark cycle: E Con[1] = eyes intact, pineal intact; E Px = eyes intact, pinealectomized; Ex Con = enucleated, pineal intact; Ex Px = enucleated, pinealectomized.

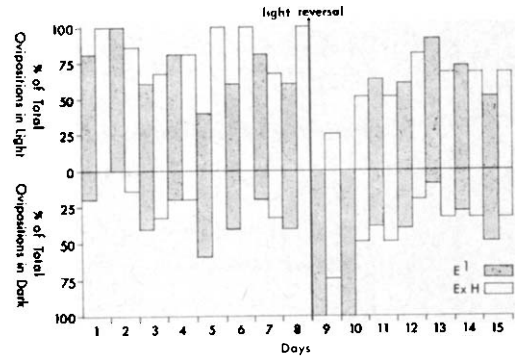

FIG. 2. Oviposition time of enucleated hooded (Ex H) and eye intact (E^1) white leghorns before and after reversal of 12-hr light and 12-hr dark cycle.

of the light–dark cycle, oviposition time remained entrained to the previous light–dark cycle for 3–4 days. After 4 days the oviposition cycle had reversed and oviposition was predominantly in the light phase of the new light–dark cycle. These data show that neither the eye nor pineal gland are necessary for entrainment of the oviposition time by the light–dark cycle. The response of the pineal in enucleated–ganglionectomized chicks demonstrates another case of extraretinal photostimulation (11). However, the oviposition response in the enucleated-pinealectomized treatment indicate the photoperiodic response in the pineal is not necessary for photoperiod entrainment of oviposition time.

The oviposition response in the enucleated–pinealectomized birds does not exclude perception of the photoperiod at the hypothalamic level (10) and was the reason for the second light reversal with hooded birds. Reversal of the light–dark cycle again resulted in a reversal of the oviposition time in all the treatments (Fig. 2). During this second light–dark reversal, the intensity of egg production had decreased and the oviposition response was not representative of as many individuals as the first reversal. However, the same pattern of response was followed. After the reversal of the photoperiod cycle, oviposition time remained entrained to the previous cycle for about 3 days and then began to predominantly occur in the light phase of the new light–dark cycle.

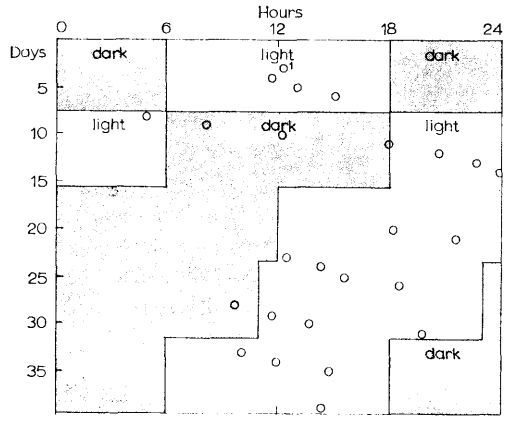

FIG. 3. Typical oviposition pattern follow reversal and lesser shifts of 12-hour light and 12-hour dark cycle: (O^1), data from eyes intact, pinealectomized white leghorn pullet.

A typical individual hen recording of oviposition pattern following the first light reversal and the subsequent shifts in photoperiod is shown in Fig. 3. Oviposition for this bird occurred in the new light period within 4 days following the photoperiod reversal. Oviposition remained in the light period of the cycle by following the respective 6-, 1- and 5-hr shift in photoperiod.

The greater length of time between successive eggs during the dark period, following the photoperiod reversal and prior to entrainment to the new light period, suggests that the oviposition cycle may function at a different rate during the dark phase of the light–dark cycle. This pattern of a greater interval between successive eggs in the dark was observed for several of the birds, regardless of pineal or eye treatment. Another interesting characteristic of oviposition time is its pattern when entrained to the light cycle. Unlike the entrained activity patterns of sparrows (18), successive eggs within a sequence occurred at a later time each day. This pattern of oviposition has been described in several reports and hypotheses have been suggested for the type of mechanism involved in this oviposition pattern (5). Oviposition cycle shown in Fig. 3 is somewhat free-running, even though entrainment to the light period of the light–dark cycle.

After exposure to continuous light, time of oviposition was distributed throughout the 24-hr period (Fig. 4). Most of the birds showed a definite free-running oviposition pattern in continuous light with 16% having an interval between successive ovipositions less than 24 hr and 84% greater than 24 hr.

Examples of oviposition pattern for the four treatments in continuous light is shown in Fig. 5. Lack of persistency in egg laying on consecutive days does not give conclusive evidence with respect to the relationship between pineal and free-running oviposition time in continuous light. However, a definite time period relationship was noted in some of the pinealectomized and enucleated–pinealectomized birds (Fig. 5). Further experiments using birds in a higher rate of egg production would be required to determine if the pineal is involved in clock mechanisms related to oviposition as it is in activity patterns of sparrows (18).

Temperature and sound level in the chambers indicated that oviposition response was not affected by these variables. Maximum temperature fluxuation was 5.0° and was not directly correlated with the chamber light–dark cycle. Sound level was different in the two chambers. There were less bird sounds in the chamber with enucleated birds at all hours of light–dark cycle. After the lights were off, both chambers recorded very little bird noise. In the chamber with enucleated birds, the dark sound level stayed about the

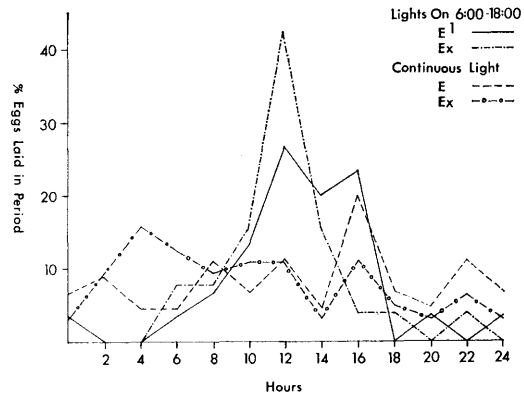

FIG. 4. Oviposition pattern of eye intact and enucleated white leghorns in a 12-hr light and 12-hr dark cycle and in continuous light: E^1 = eyes intact; Ex = enucleated.

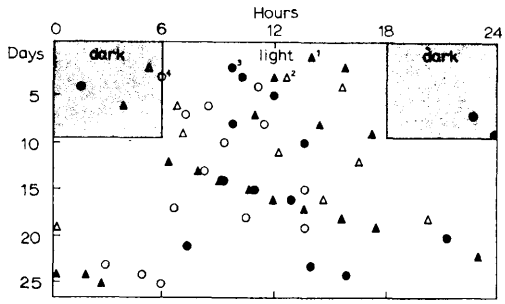

FIG. 5. Oviposition time and pattern during and following a change from a 12-hr light and 12-hr dark cycle to continuous light: (▲[1]), enucleated, pineal intact (bird no. 37); (△[2]), enucleated, pinealectomized (bird no. 48); (●[3]), eyes intact, pineal intact (bird no. 7); and (○[4]), eyes intact, pinealectomized (bird no. 2).

same until ovipositions began to occur, 2–3 hr after the lights were on. However, in the chamber in which the eyes were intact, bird sound immediately increased following the transition from dark to light.

Summary. Oviposition response to photoperiod was studied in normal, pinealectomized, enucleated, and enucleated–pinealectomized chickens. Oviposition pattern in all of the treatments responded to reversal and shifts in the light–dark cycle. Hooded enucleated and enucleated–pinealectomized birds showed the same oviposition response to light reversal as the birds with eyes intact. Oviposition pattern, though entrained by the photoperiod, indicated a definite pattern within the photoperiod. Some birds in all of the treatments exhibited a free-running circadian pattern of oviposition in continuous light. These data demonstrate that photocontrol of oviposition in the chicken occurs without eyes or pineal and that the pineal is not necessary for free-running circadian pattern of oviposition.

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