

TABLE II. Young Ducklings Infected with Ornithosis Virus and 10 Days Later Challenged with Malaria. Mild ornithosis. Combined results of 10 experiments.

	Test	Control
No. of ducklings used	130	52
" surviving ornithosis infection	130	
" " malaria challenge	126	4
% " malaria challenge	97	7.7
% having mild parasitemia	98	2

and liver (due to ornithosis) is always present

in resistant ducklings.

Summary. 1) Ducklings infected with ornithosis 6 to 14 days before a challenge dose of *P. lophurae* malaria parasites exhibit a marked resistance to the challenge. 2) The resistance is associated with increase of the reticulo-endothelial elements in the enlarged liver and spleen due to the ornithosis infection.

Received April 24, 1957. P.S.E.B.M., 1957, v95.

Oviduct Response to Estrogen and Progesterone in the Ring Dove (*Streptopelia risoria*).^{*} (23226)

DANIEL S. LEHRMAN AND PHILIP BRODY (Introduced by F. A. Beach)

Department of Psychology, Rutgers University, Newark, N. J.

Both antagonistic(1) and synergistic(2,3, 4) effects of progesterone and estrogens on weight of the oviducts of domestic hens have been reported. Mason(5) showed that the amounts and dosage ratios of estrogen and progesterone determined, in part, whether an antagonistic or synergistic effect would be observed. Furthermore, the 2 hormones appear necessary for normal oviduct development, as estrogen alone causes gland growth but progesterone in the presence of estrogen induces formation of secretion granules in the magnum(4).

In the course of a study of the hormonal induction of incubation behavior in the ring dove(6), behavioral effects of the hormones were found which suggested that the normal course of nest-building and incubating behavior depends upon the *successive* effects of estrogen and progesterone. The present study was undertaken to determine whether the effects of estrogen and progesterone on oviduct weights in this species are consonant with the hypothesis that progesterone is secreted after a period of estrogen secretion.

Methods. Sixty-three female ring doves (*Streptopelia risoria*), approximately 4 months of age, were selected for the experiment on

the basis of direct examination of the ovary and oviduct through an incision in the abdominal wall. All had first and second phase ovules and undeveloped oviducts, and were thus not quite mature(4,7). The mean body weight was 148.7 g, S.D. 15.2 g. The substances used were injected (in 0.1 ml sesame oil) into the pectoral muscles on alternate sides from day to day, for 10 days. On the day following the last injection, the birds were killed by an overdose of pentothal sodium, and the oviducts removed and weighed. Groups of 9 birds each were treated as follows: 1) Control. 0.1 ml sesame oil daily x10. 2) Progesterone. 0.1 mg daily x10. 3) Estrogen. 0.4 mg diethylstilbestrol daily x10. 4) Progesterone + Estrogen. 0.1 mg progesterone plus 0.4 mg diethylstilbestrol daily x10. 5) Control primed. 0.1 ml sesame oil daily x8, followed by 0.1 mg progesterone plus 0.4 mg diethylstilbestrol daily x2. 6) Progesterone primed. 0.1 mg progesterone daily x8, followed by 0.1 mg progesterone plus 0.4 mg diethylstilbestrol daily x2. 7) Estrogen primed. 0.4 mg diethylstilbestrol daily x8, followed by 0.1 mg progesterone plus 0.4 mg diethylstilbestrol daily x2.[†]

^{*} This study was supported by grants from National Science Fn. and the Rutgers University Research Council.

[†] Progesterone ("Lutocyn," Ciba) was supplied through the courtesy of Dr. Robert Gaunt of CIBA. Diethylstilbestrol was supplied through the courtesy of Dr. Aleck Borman of E. R. Squibb and Sons.

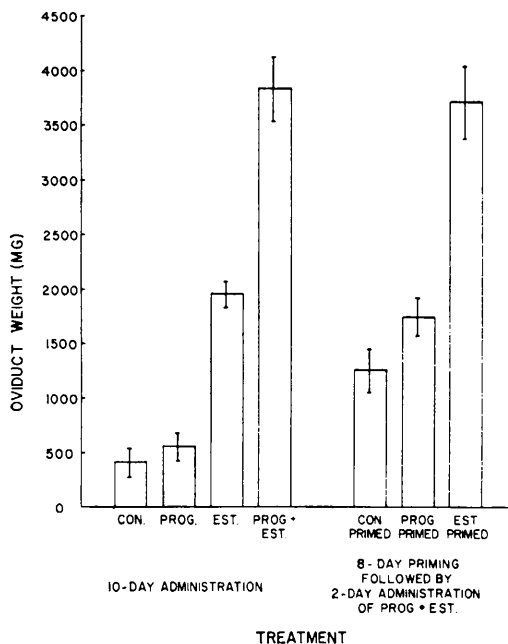


FIG. 1. Effect of hormone treatment on oviduct weights of ring doves. Length of vertical bars = 2 standard errors of mean (9 birds/group). Con. = Control (sesame oil). Prog. = Progesterone. Est. = Estrogen (diethylstilbestrol) (see text).

Results. The oviduct weights are presented in Fig. 1. Differences between all groups were tested for statistical significance by the Mann-Whitney U test(8), and the results of the comparison are shown in Table I.

Progesterone administration, in the dosages used, did not increase oviduct weights. Estrogen, however, significantly enhanced oviduct weight, and the combined administration of progesterone and estrogen caused a striking and significant increase over the effect of estrogen alone. These differences are easily discernible on gross examination of the oviducts. The dosage ratio of 4 estrogen/1 progesterone is one that had been reported by Mason(5) to have synergistic effects.

Priming for 8 days with estrogen, followed by 2-day administration of the estrogen-progesterone combination, caused as much oviduct growth as did 10-day administration of the combination. The weights of these oviducts were comparable to the maximum weights achieved in a normal breeding cycle. On the other hand, priming for the same period with progesterone did not significantly

increase the effect of the 2-day administration of the 2-hormone combination, and caused much less oviduct growth than the 10-day administration of the combined dose.

Discussion. These data suggest that the normal growth of the oviduct, which reaches a sharp peak just after the laying of the first of the 2 eggs(9), could be accounted for by assuming the secretion of estrogen which causes moderate increase in weight, followed by secretion of progesterone for a short time, causing a sharp increase in weight.

There are other sources of evidence which support such a hypothesis of the ovarian picture in the nesting female ring dove. Fraps (10) reports that a single injection of progesterone into a laying hen will stimulate the premature release of an egg by the ovary. If progesterone is normally so involved in egg-laying in the ring dove, we might tentatively assume the occurrence of progesterone secretion just before ovulation of the first egg, which could account both for the ovulation and for the greatly increased oviduct growth which is observed at this time(9). Since the progesterone seems to stimulate ovulation via release of pituitary LH, however, there would still remain a number of questions concerning the initial stimulation of progesterone secretion.

Observations of nesting and incubating behavior suggest the same pattern. Estrogen injection has the same effect as does participation in courtship upon the behavior toward eggs subsequently introduced into the cage: it induces intensive nest-building, followed

TABLE I. P-Values for Comparison of Oviduct Weights of Groups of Ring Doves. Mann-Whitney U test. The first-named group in each pair had the larger mean oviduct wt.

Groups compared	P
Progesterone + estrogen vs estrogen primed	>.10
Progesterone vs control	>.10
Estrogen " "	<.002
Progesterone + estrogen vs control	"
Estrogen vs progesterone	"
Progesterone + estrogen vs progesterone	"
" + " estrogen	"
Progesterone primed vs control primed	>.10
Estrogen " " " "	<.002
" " " progesterone primed	"

after 1-3 days by incubation(6,12). Progesterone injection has the same effect as does participation in courtship and nest-building: it induces immediate incubation(6,11). This suggests that the normal cycle may include a period of nest-building (associated with estrogen secretion), which induces a subsequent period of incubation (the beginning of which is associated with progesterone secretion).

Brant and Nalbandov(4) state that, since androgen also has synergistic effects with estrogen on oviduct growth, and since androgen has been found in the fowl ovary(13), the physiological substance involved in oviduct growth may be androgen rather than progesterone. While this is possible, several considerations suggest that the physiological involvement of progesterone should be further explored: 1) Progesterone has been found in the blood of hens and roosters(14,15); 2) Androgen stimulates male sexual behavior, which is antagonistic to the broodiness induced by progesterone and normally occurring at the time of egg-laying and of maximum oviduct growth(16,17); 3) Although testosterone and progesterone both augment the effect of estrogen on oviduct weight in hens, the effect on female sexual behavior in the same birds is that progesterone augments the effect of estrogen, while androgen does not(2); 4) Progesterone causes immediate incubation in all doves treated, while androgen does not(9). Progesterone, unlike androgen, can thus account for both the behavioral and the morphological changes which take place at about the time of egg-laying.

Summary. 1. Adolescent female ring doves (*Streptopelia risoria*) were injected with progesterone, estrogen or a combination of the two. Progesterone did not increase oviduct weights over the controls. Estrogen caused moderate increase, while the maximum increase was caused by synergism between estrogen and progesterone. 2. Eight-day priming with estrogen, followed by 2-day treatment

with the estrogen-progesterone combination, caused oviduct growth as great as that caused by the 10-day treatment with the combined dose. On the other hand, priming with progesterone did not significantly augment the effect of 2-day treatment with the combination. 3. On the basis of these data and of a discussion of the mechanisms of nest-building and incubation behavior, it is suggested that the normal cycle includes a period of estrogen secretion (concurrent with nest-building) followed by progesterone secretion (associated with egg-laying maximal oviduct growth, and incubation behavior).

We are indebted to Dr. James Leathem for his criticisms of the manuscript, and to Mr. Daniel Wilhoit for assistance in collection of data.

1. Hertz, R., Larsen, C. D., and Tullner, W. W., *J. Nat. Cancer Inst.*, 1947, v8, 123.
2. Adams, J. L., and Herrick, R. B., *Poultry Sci.*, 1955, v34, 117.
3. Mason, R. C., *Anat. Rec.*, 1951, v111, 458.
4. Brant, J. S. A., and Nalbandov, A. V., *Poultry Sci.*, 1956, v35, 692.
5. Mason, R. C., *Endocrinol.*, 1952, v51, 570.
6. Lehrman, D. S., *J. comp. physiol. Psychol.*, in press.
7. Cuthbert, N. L., *J. Morphol.*, 1945, v77, 351.
8. Siegel, S., *Nonparametric Statistics*. N. Y., McGraw-Hill. 1956.
9. Riddle, O., *Endocrinology*, 1942, v31, 498.
10. Fraps, R. M., *Mem. Soc. Endocrinol.*, 1955, No. 4(1), 205.
11. Riddle, O., and Lahr, E. L., *Endocrinol.*, 1944, v35, 255.
12. Lehrman, D. S., *J. comp. physiol. Psychol.*, in press.
13. Taber, E., *Endocrinol.*, 1951, v48, 6.
14. Fraps, R. M., Hooker, C. W., and Forbes, T. R., *Science*, 1948, v108, 86.
15. ———, *ibid.*, 1949, v109, 493.
16. Bennett, M. A., *Ecology*, 1940, v21, 148.
17. Nalbandov, A. V., and Card, L. E., *J. Hered.*, 1945, v36, 35.

Received April 24, 1957. P.S.E.B.M., 1957, v95.