THE CONDOR

VOLUME 43 SEPTEMBER-OCTOBER, 1941 NUMBER 5

AN EXPERIMENTAL ANALYSIS OF THE BREEDING CYCLE OF THE TRICOLORED RED-WING

By JOHN T. EMLEN, JR.

It is generally agreed that the awakening or release of any particular behavior pattern is dependent upon two conditions: (1) an appropriate physiological state in the subject, and (2) a timely external stimulus. In birds, certain aspects of behavior, particularly those associated with breeding, pass through a cycle of striking changes as the season advances. These changes in behavior are paralleled by equally definite physiological and environmental changes, so that each stage in the behavior cycle has its characteristic internal and external concomitants.

The internal or physiological changes which occur during the year are reflected in the size, structure and activity of various organs of the body (see Riddle, 1938: 266-270), but are best defined for present purposes in terms of the behavior reactions which they underlie. Thus incubating behavior is the direct expression of a physiological condition variously referred to by writers as the incubation "drive," "impulse" or "urge." This drive, as with those that precede or follow it in the breeding cycle, is clear-cut and regular in its appearance and duration under normal circumstances. Although each of the specialized behavior patterns of the breeding season is closely related to the corresponding physiological condition, the two are not inseparable. Whitman (1919) and others have repeatedly demonstrated that a drive may exist unexpressed in the absence of an appropriate external stimulus.

The external stimuli with which we are here concerned are the specific situations in the physical environment which serve as the objectives of activity for each stage in the breeding cycle. A nest with eggs, for instance, is the specific situation toward which incubation behavior is directed. Nestlings are, in the same way, the direct objective of feeding-the-young behavior. Each of these situations is the product of activity of an earlier stage of the same breeding cycle. Thus a completed nest, which is associated with laying behavior, is created by the birds themselves during the preceding (nest-building) stage of the breeding cycle; a set of eggs, which is related to normal incubation behavior, is a direct product of egg-laying activity; and so on. Each external situation is thus seen to be dependent for its existence on the preceding stages of behavior, and each in turn functions to supply pertinent equipment to the cycle at the appropriate moment.

It is obvious that this succession of external situations is closely interrelated with the internal or physiological rhythm, and that for normal development the two must progress along parallel courses in harmonious synchrony. In the present study this synchrony was experimentally disrupted by modifying the normal progress of the external succession. By thus separating external stimuli from their normal internal concomitants, information was obtained on the degree of independence of the internal cycle, and on the significance of external situations as releasing agents.

The Tricolored Red-wing (*Agelaius tricolor*) was selected as the subject for study because of the ready availability of large numbers of nests within conveniently circumscribed limits (see Neff, 1937). Experiments were conducted in the spring of 1940 on 204 nests of this species in two colonies in the Sacramento Valley of California, one near

Hammonton with about 7000 nests and the other near Arboga with about 15,000 nests. Supplementary experiments were conducted on 26 nests of the Brewer Blackbird (*Euphagus cyanocephalus*) at Davis. Behavior responses were determined primarily through circumstantial evidence of activity; direct field observations, unfortunately, were limited.

Normal Behavior Cycle.—The temporal relations of stages in the breeding cycle of the Tricolored Red-wing are diagrammed in table 1. Mutual mating responses with coition usually appear at least 4 days before egg laying, and are continued until the commencement of incubation when nearly all the males leave the nesting environs (Lack and Emlen, 1939: 227). Nest building is performed entirely by the female and usually requires 2 to 5 days for the first nesting, and 4 (3 to 5) for the second. In a typical four-day nest-building period, the first day is spent in constructing the basal platform, the second in rounding up the sides, the third in forming the mud and wet vegetation, and the fourth in lining and completing the nest. The first egg is usually laid the day after building is finished. One egg is deposited each day for 3 or 4 days. Incubation behavior, confined to the female, usually starts with the laying of the last egg, or on the succeeding day, and continues for 11 (10 to 12) days before the eggs hatch; it then continues as a brooding response to nestlings, for at least 3 or 4 days more. Both sexes participate in feeding the young, the males reappearing at the appropriate time. Young are fed for 10 to 12 days in the nest and then for at least two weeks more in the nest vicinity.

TABLE 1

Schedule of behavior stages in the breeding cycle of male and female Tricolored Red-wings as related to changes in the external situation at the nest site. The beginning of a second cycle is indicated for the female.

<table>
<tr><td>Time in days</td><td colspan="2">5</td><td>10 15</td><td>20 25</td><td>30 35</td></tr>
<tr><td rowspan="2">Situation at nest site</td><td colspan="2">A Responsive Mate</td><td rowspan="2">Nest with complete set of eggs</td><td rowspan="2">Nest with young</td><td rowspan="2">Young in nest vicinity</td></tr>
<tr><td>Incomplete nest</td><td>Unfilled nest</td></tr>
<tr><td>Activities of male</td><td colspan="2">Mating</td><td>(Absent)</td><td>Feeding of nestlings</td><td>Feeding of fledglings</td></tr>
<tr><td rowspan="2">Activities of female</td><td colspan="2">Mating</td><td rowspan="2">Incubating</td><td rowspan="2">Brooding
Feeding of nestlings</td><td>Feeding fledglings</td></tr>
<tr><td>Building</td><td>Laying</td><td>Building | Laying</td></tr>
</table>

Nests for second layings are started a day or two before the young of the first brood in that section of the colony leave their nests, and egg-laying begins about four days later. New nests for second layings are the rule, but old nests are occasionally built up and reoccupied. Birds were not individually marked, so it is not certain that second nests belonged to the same adults. Observations on behavior, however, support such an interpretation.

Mating.—No attempt was made in the present study to control or manipulate the elusive environmental factors associated with the release of the various phases of mating behavior, except as discussed later under "nest-building" and "egg-laying." A brief review of present knowledge of the subject, however, is in order.

The disposition to mate has been shown to develop under the influence of secretions of the pituitary, as when stimulated through increased exposure to light, until an advanced condition of gonadal development and of sexual responsiveness is attained

(Marshall, 1936: 435; Bissonnette, 1938: 246-254). The development of this condition into the final phase of mating behavior, however, seems to require the releasing action of an appropriate environmental situation in many birds. Thus a condition of sexual maturity, as judged by histological criteria, is inadequate to induce ovulation in female pigeons unless a male or some acceptable substitute is present to provide a stimulus through courtship, posturing and reciprocal mating behavior (Harper, 1904; Craig, 1911, 1913; Matthews, 1939) or through its mere presence (Patel, 1936: 145). This dependence on mates for the final stimulus to ovulation apparently is a fairly common phenomenon among birds (Marshall, 1936: 445; Bissonnette, 1939: 230). Other external factors, however, may also play a rôle in releasing the final stage of mating behavior. Certain captive parrots, for instance, will not pair or breed unless an artificial nest is provided in their cage (Manteifel, 1937). English robins may fail to breed if they are unsuccessful in establishing territorial claims (Lack, 1940: 264). Gulls that nest in colonies are influenced in their mating responses by the social stimulus of other members of the nesting flock (Goethe, 1937; Darling, 1938; Richter, 1939). Tricolored Red-wings probably also depend to a certain extent on mutual stimulation from colony associates, for the members of each nesting group show a marked simultaneity in breeding which is completely lacking as between different groups (Dawson, 1923: 113; Neff, 1937: 76; Lack and Emlen, 1939: 227).

Male birds are generally less dependent on environmental releasers for mating behavior than are females (Bissonnette, 1939: 230), but, at least in the pigeon, they may fail to exhibit the complete response until socially stimulated (Craig, 1914: 31).

Nest-building.—Nest-building behavior in female birds is usually closely related to mating, and in the Tricolored Red-wing, as in various other species (Howard, 1929, 1935); Tinbergen, 1939: 29), coincides with the short period of reciprocal mating behavior which immediately precedes egg-laying.

A relationship between this period in the behavior cycle and the final period of rapid ovular growth in the physiological cycle (Riddle, 1916) is suggested by various observations. Studies with pigeons, for instance, show that a sudden acceleration of physiological processes initiating the final period of ovular growth occurs 6¼ days before the first egg is laid (108 hours before ovulation, according to Riddle, 1938: 268, plus 42 hours before laying, according to Harper, 1904). The period of active reciprocal mating in these birds commences at almost exactly the same time, 6 to 7 days before laying (Whitman, 1919:3). Allen's (1914) data on the Red-winged Blackbird show a six-day period of rapid ovarian growth (plate 21) and a six-day period of nest building behavior (page 98). A similar coincidence of physiological activity and nest building behavior occurs in the Tricolored Red-wing (Emlen, unpublished data).

Experiments undertaken in the present study were designed to test the influence of nest stimuli on the duration of nest-building behavior and on the inception of laying which, under normal circumstances, marks its termination. Attempts were made to shorten the period by artificially accelerating the completion of nests. This was done by substituting advanced or finished nests at the site of newly begun structures. Prolongation of the period was essayed by robbing nearly completed nests of component materials. Similar experiments were performed on completed nests containing eggs or young to test the birds' inclination to return to nest-building behavior after laying had started.

Satisfactory results were obtained from 20 experiments. Nest desertion was frequent in the less advanced nests and accounted for 15 failures. Five experiments in which the lateral lining of nests was incompletely removed were unsatisfactory because of subsequent difficulty in differentiating new material from grasses trampled in from the nest margins.

The results of observations and experiments on nest building in the Tricolored Redwing (table 2) may be summarized as follows:

1. The period of nest-building activity normally covers the 4 (3 to 5) days before laying starts (13 control nests) and does not reappear thereafter (table 2, experiments 22 to 29, 32 to 40; see comments under "egg-laying" for interpretation of experiment 21).

2. Laying occasionally starts before the nest is completed. Under such circumstances construction may be extended for at least one day (table 2, experiments 17, 18; also see Dawson, 1923: 111).

3. Eggs or young artificially introduced into an incompleted nest will not necessarily interrupt the normal course of nest-building activity (table 2, experiments 13, 14, 15).

TABLE 2

Experiments with nest-building responses (second nestings)

No.	Stage of construction	Experiment	Result
1	Basal platform (1st day)	¾ constructed nest substituted	abandoned
2		½ constructed nest substituted	abandoned
3		½ constructed nest substituted	abandoned
4		completed nest substituted	laid after 3-day rest
5	Sides rounded up (2d day)	completed nest +2 eggs substituted	abandoned
6		completed nest +2 yg. substituted	
7		½ the material removed	
8		½ the material removed	
9		½ the material removed	
10	Ready for lining (3d day)	lining added	
11		lining +1 yg. added	laid after 2-day rest
12		lining +2 yg. added	abandoned
13		1 egg added	lining completed, egg next day
14		3 eggs added	lining completed, egg next day
15		2 young added	lining completed, egg next day
16		2 young added	abandoned
17	Ready for lining (1 egg)	....	lining partially completed next day
18		....	lining partially completed next day
19	Nest completed (4th day)	reduced to platform	abandoned
20	Nest completed (1 egg)	lining removed	abandoned
21			lining replaced, laid 5 eggs
22			no new material added
23			
24			
25			
26			
27			
28			
29			*
30	Nest completed (2 eggs)		abandoned
31			abandoned
32			no new material added
33			
34			
35			*
36	Nest completed (3 eggs)		
37			
38			*
39	Nest completed (4 eggs)		*
40	Nest completed (incub. advanced)		*

*Small amount of lining material present probably due to incomplete removal of lateral lining.

4. Four attempts to delay nest completion by artificial means were unsuccessful, but in two colonies where nest construction was interrupted or delayed by natural factors the birds commenced laying without regard to the incompleteness of their nests (Dawson, 1923: 111; Neff, 1937: 76).

5. Artificial completion of nests ahead of schedule did not hasten the commencement of laying but did relieve the owners of from one to three days of labor in nest construction (table 1, experiments 4, 11).

Egg-laying.—The duration of egg-laying behavior in the Tricolored Red-wing may be deduced from the size of the clutch, since the normal laying rate in all nests observed (one exception, see below) was one per day. Undisturbed nests in mid-incubation in the colonies under study contained 4 eggs in 87 instances, 3 eggs in 47 instances and 2 eggs in 7 instances, making an average of 3.6 eggs per nest. Some of the sets of 2 and 3 may have been reduced from a higher number through losses subsequent to laying, as attested in the records of a number of experimental nests. No natural sets of 5 eggs were seen, although nests with 5, 6 and even 7 have been recorded for the species by Dawson (1923: 110).

The factors which govern the cessation of laying in birds are poorly understood. Certain species of gallinaceous birds, ducks, woodpeckers and passerines lay until an accumulation of eggs releases the incubation response (Groebbels, 1937: 243; Marshall, 1936: 443; Pearl, 1912: 158). These birds have been termed "indeterminate layers" by Cole (1917: 504) in accordance with their ability to continue laying indefinitely if their eggs are removed from the nest as laid. In other species, including certain pheasants, doves, pigeons and passerines, the size of the clutch, and hence the duration of the laying period, is apparently predetermined by intra-organic factors when egg-laying is begun (Craig, 1913: 219). This group Cole terms "determinate layers."

Experiments to determine the effects of egg accumulation on the duration of laying in the Tricolored Red-wing were of two types: (1) attempts to prolong the period by removing eggs, and (2) attempts to shorten it by artificially filling out incompleted sets.

Definite results were obtained from 62 of the 119 experiments undertaken. Of the 57 nests that failed to produce reliable information, 19 were abandoned before results could be read; 16, according to subsequent observations, had been partially incubated at the time of manipulation; and 22 were disturbed by natural causes.

The results of these experiments show that the Tricolored Red-wing is a determinate layer, that is, the egg-laying period cannot be prolonged by the process of removing eggs from the nest during laying. This was borne out in 10 of the 12 completed nest-robbing experiments (table 3, experiments 48-62). Both exceptions represent atypical conditions. One (no. 62) was probably complicated by the laying of two females, since three eggs, one of them larger than the others, appeared in the nest in 2 days. The other (no. 51) was peculiar in being the only instance in which a resumption of nest building was induced (by removal of the lining) after an egg had been laid in a completed nest (see table 2, no. 21). It seems likely that the second irregularity of behavior in this instance was related to the first. If the clutch in determinate layers is released as a predetermined unit, as suggested by Craig (1913: 219), it is possible that the egg-laying period in this instance was recommenced or advanced a day after an initial start had been "called back" by further, artificially induced, nest-building activity.

Premature completion of the clutch with artificially introduced eggs failed to influence the length of the laying period in 34 out of 42 satisfactory experiments (table 3, nos. 1-47). In the remaining eight experiments (table 3, nos. 1, 2, 11, 16, 20, 22, 34, 40), however, a subnormal number of eggs (2) was laid, and in 6 of these the accumulated total was only 3 or 4. The average number of eggs laid in all supplemented nests

TABLE 3

Experiments with adding or removing eggs during the laying period

	Experiment			Results		Deductions
	a	b	c			
Experiment No.	Number of eggs at start of experiment	Eggs removed (−) or added (+)	Eggs in nest after manipulation (a+b)	Eggs in nest after incubation had started	Number of eggs laid	Laying affected by manipulation
1	0	+1	1	3	2	Yes
2	0	+1	1	3	2	Yes
3	0	+1	1	5	4	No
4	0	+1	1	5	4	No
5	0	+1	1	4	3	?
6	0	+1	1	4	3	?
7	0	+2	2	6	4	No
8	0	+2	2	5	3	No
9	1	+1	2	5	4	No
10	1	+1	2	4	3	?
11	1	+2	3	4	2	Yes
12	1	+2	3	5	3	No
13	1	+2	3	6	4	No
14	1	+2	3	5	3	No
15	1	+2	3	6	4	No
16	1	+2	3	4	2	Yes
17	1	+2	3	5	3	No
18	1	+2	3	6	4	No
19	1	+2	3	5	3	No
20	1	+3	4	5	2	Yes
21	1	+3	4	6	3	No
22	1	+3	4	5	2	Yes
23	1	+3	4	6	3	No
24	1	+3	4	6	3	No
25	1	+3	4	6	3	No
26	1	+3	4	6	3	No
27	1	+3	4	6	3	No
28	1	+3	4	6	3	No
29	1	+3	4	6	3	No
30	2	+1	3	5	4	No
31	2	+1	3	5	4	No
32	2	+1	3	4	3	?
33	2	+1	3	5	4	No
34	2	+2	4	4	2	Yes
35	2	+2	4	5	3	No
36	2	+2	4	6	4	No
37	2	+2	4	5	3	No
38	2	+2	4	6	4	No
39	2	+2	4	5	3	No
40	2	+2	4	4	2	Yes
41	2	+2	4	6	4	No
42	2	+2	4	5	3	No
43	2	+2	4	6	4	No
44	2	+2	4	5	3	No
45	2	+3	5	7	4	No
46	3	+1	4	5	4	No
47	3	+1	4	4	3	?
48	4	−2	2	2	4	No
49	3	−2	1	2	4	No
50	3	−2	1	2	4	No
51	3	−2	1	3	5	Yes
52	3	−2	1	2	4	No
53	3	−2	1	2	4	No
54	3	−2	1	1	3	No
55	3	−2	1	2	4	No
56	3	−2	0	1	4	No
57	2	−1	1	3	4	?
58	2	−1	1	2	3	No
59	2	−1	1	2	3	No
60	2	−1	1	3	4	?
61	2	−1	1	3	4	?
62	2	−1	1	4	5	Yes

was 3.3 as compared with 3.6 in undisturbed nests, and where as many as 3 eggs were introduced, the birds laid an average of only 2.8. There was, thus, a tendency toward smaller clutches in some of the supplemented nests, particularly those treated early in laying. This may represent either a slight response by the bird to eggs in the nest, or an increased loss of eggs through accidents attendant on an overcrowded nest. The latter possibility must not be overlooked, for when more than 5 eggs are present, they generally become arranged in two tiers, bringing the upper eggs perilously close to the nest rim.

Observations and experiments on egg-laying may be summarized as follows:

1. The duration of the egg-laying period is generally 3 or 4 days; one egg is laid each day.
2. The laying period was not prolonged by artificial removal of eggs from the nest during laying and was shortened only slightly if at all by addition of eggs to the nest during laying.

3. The rate and duration of egg-laying was not affected by: (a) removal of nest lining (13 instances, no exceptions); (b) the hatching of previously introduced eggs in the nest (1 instance, no exceptions); (c) the presence of artificially introduced nestlings being fed by the male (4 instances, no exceptions, 2 questionable records).

Incubation.—The transition from the laying stage to the incubation stage forms an important turning point in the breeding cycle of birds. Riddle (1938: 267) remarks: "One may hope to witness few more striking changes in an animal than those involved in the passage of a pigeon from the copulatory to the broody phase; yet the time interval between the two phases may be no more than 48 hours." Whitman (1919: 104) concluded from his studies that "incubation and sexual activity are mutually exclusive and antagonistic phenomena" and that they "never occur together" in the pigeon. Mating behavior has been observed during the incubation period in a few wild birds (Kirkman, 1937: 197; Schüz, 1932: 20; Witherby, et al., 1938: 14), but it is definitely a rare phenomenon. Riddle and Bates (1930: 695) believe that prolactin, the hormone of the incubation period, acts to suppress the endocrine activity of the gonad in pigeons, and suggest that some such gonad inhibiting factor must be present during incubation in all birds "which nest their eggs."

Sexual activity, although it is generally submerged as soon as incubation sets in, apparently performs an important function in conditioning the bird for incubation behavior, for incubation rarely appears except as a sequel to mating behavior. The male of a pair has been known to display incubation behavior before its mate has laid (Howard, 1935:6; Watson, 1908:223), but the absence of eggs is no criterion of sexual unpreparedness in a male bird. Whitman (1919: 103) observed no instances in his pigeons where a bird manifested a broody impulse without previous sexual activity, and he believed that incubation behavior was "a physiological outgrowth of these former acts." Patel (1936:145) found that removal of the gonads in male pigeons did not alter the incubation behavior which followed in the same cycle but apparently precluded subsequent expression of normal incubation behavior. In experiments with prolactin injections, Riddle (1937: 223) observed that sexually conditioned (laying) chickens responded more readily than did non-laying birds.

A nest containing eggs or egg substitutes (Friedmann, 1934: 33; Kirkman, 1937: 89) is generally necessary for the release of incubating behavior in birds. Exceptions, however, are not uncommon; domestic poultry and pigeons occasionally react in a broody manner to inanimate objects or even to a bare floor. Howard (1935) cites several instances in which nests of wild birds continued to elicit the broody response after their contents had been removed, and Patel (1936:134) has demonstrated that the mere sight of a brooding mate through a partition may be adequate to arouse and maintain incubation behavior in pigeons.

The stimulus to incubate produced by the sight of a nest with eggs may be very strong. Taibell (1928) induced broodiness in a turkey cock merely by tying it to a nest with eggs. Watson (1908:223), by introducing an egg into an empty nest, induced the incubating response in a male tern a week before its mate had laid.

The influence of the presence of eggs on the duration and continuity of the incubation period is profound. Terns have been caused to extend their incubating response as much as 7 days and to shorten it by a similar amount (Lashley, 1915: 82). Domestic hens have been known to sit on dummy eggs for as long as 4 months (Hillwald, cited in Katz, 1937: 150). Leverkühn (1891: 30) induced a Marsh Harrier to incubate continuously for 8½ weeks. A Black-headed Gull sat on a wooden egg for 75 days (Kirkman, 1940). Pigeons and doves will sit for an average of 4 to 6 days beyond the normal hatching date despite restrictions imposed by maturing of the "crop glands" (Cole and Kirkpatrick, 1915: 502-506). Game keepers in Europe recognize and make use of the flexibility of the incubation stage when they practice the "Euston system" of substituting well incubated eggs for freshly laid clutches (Maxwell, 1911: 109) in order to reduce the sitting period and hence the incidence of egg destruction.

Several workers have demonstrated that incubation behavior may be recalled after a brief interruption. Lashley (1915: 80) found that by returning eggs to robbed nests he could revive the incubating instinct in terns 4 days after it had been interrupted; he states that in many cage birds this period of suspension may be extended to more than a week. Patel (1936:139) found that in pigeons the development of the "crop glands," which is closely related to broody behavior, could be checked and started again several times by alternating the presence and absence of nest stimuli.

The brooding of nestlings should perhaps be included under incubation since it bears a closer resemblance and probably a closer relationship to sitting on eggs than to feeding of nestlings. Howard (1935: 32, 42) presents evidence for this relationship in his experiments with European Linnets and Yellow Buntings in which the nestlings, placed in an adjacent nest drew the feeding reactions of the parents while the empty old nest continued as the objective of sitting behavior.

In the Tricolored Red-wing, incubation behavior occurs only in the female. It normally extends through an 11-day period until the eggs hatch and then continues in gradually diminishing intensity for at least 3 or 4 days more as a brooding response to nestlings. Males are generally absent from the colony until the eggs hatch and they assist only in feeding operations thereafter.

In 23 experiments on Tricolored Red-wing nests, eggs far advanced in incubation were introduced into nests containing fresh eggs. In all of these the new eggs were accepted and the young which hatched a day or so later deflected the entire attention of the "parents" away from their own eggs. Thus, the period devoted to incubation of eggs was reduced from the normal 11 (10 to 12) days to 6 (2 instances), 5 (2 instances), 3 (1 instance), 2 (4 instances), 1 (4 instances), and 0 (7 instances) days; three experiments were inconclusive. Eggs laid by the nest owner in these 23 nests failed to hatch because of the premature cessation of incubation, but in 4 other nests where the introduced eggs were only 2, 2, 2 and 4 days, respectively, ahead of the owner's, eggs from both groups hatched.

Nestlings 2 to 3 days of age were introduced into 10 nests where the laying phase was just being completed. In 2 of these the old birds deserted, in the other 8 the strange nestlings took precedence over the eggs, and the nest owners passed directly from laying into the feeding-the-young stage.

Two incomplete attempts were made to extend the period of incubation behavior beyond the normal. In one nest the substitution of fresh eggs for a partially incubated clutch delayed hatching by 3 days. In the other a sterile egg was accepted in place of the single day-old nestling and incubated for 2 days. Eggs substituted for 2-day old nestlings in a Brewer Blackbird nest at Davis were accepted and incubated for 2 days before they hatched.

Observations and experiments dealing with the incubation period may be summarized as follows:

1. Incubation (sitting) behavior in the Tricolored Red-wing occurs only in the female. The normal duration is 11 days on eggs, plus 3 or more on nestlings.
2. The period of incubation behavior may be greatly reduced and even eliminated from the cycle by manipulating the nest contents.

3. The period of incubation behavior may be extended at least 3 days. No checks were made on the limits of extension.

Feeding the young.—Feeding-the-young behavior is regulated in pigeons by the appearance of "milk" in the crop which is, in turn, closely timed in relation to previous developments of the physiological cycle from mating onward (Patel, 1936:143). As a consequence any considerable advance or delay in the appearance of the young is highly disruptive (Whitman, 1919:68). In most birds, however, no such restrictive internal mechanism is in control; indeed the urge to feed young seems to be more or less independent of the rest of the breeding cycle. Non-breeding birds will, on occasion, respond to the begging-for-food stimulus, and fledglings of the first brood may assist in the feeding of the second (Skutch, 1936; Ruthke, 1939). Even pigeons may exhibit a partial response outside of the breeding cycle; Whitman (1919:68) has recorded two instances in which squabs of 11 and 12 days went through the motions of food delivery in response to the food-begging actions of nest mates.

The stimulus for feeding-the-young behavior is normally the presence of nestlings calling for food in the nest, or of fledged young similarly calling in the nest vicinity. The identity of the nestlings in the nest is apparently of minor importance in the Tricolored Red-wing, for no difficulties were encountered in transferring young from nest to nest up to the end of nestling life.

The normal feeding period of the Tricolored Red-wing may be divided into two phases: (1) feeding of nestlings in the nest and (2) feeding of fledged young in the nest vicinity. The first phase usually requires about 11 days, although nestlings may leave the nest when alarmed as early as the 9th day. A few experiments on the time limits of this phase of the cycle showed it to be very flexible. Advanced (9± days) nestlings were successfully established in place of 3-day-old young in one nest and of 2-day-old young in another. This served to reduce the feeding-of-nestlings stage from 11 to 5 and 4 days, respectively. Two-day young were introduced into one nest when the rightful young were 10 days old and the attending pair was thus induced to feed nestlings for 17 consecutive days. Feeding behavior in one nest was discontinued with the removal of the 2-day-old introduced nestling, then resumed 7 days later when the rightful eggs hatched.

Experiments described in this paper under *incubation* show that the feeding response to nestlings may be aroused in Tricolored Red-wings at any time in the laying or incubation stages of the cycle. In two nests watched from a blind the male fed the introduced nestlings during the laying stage, ceasing all singing and mating behavior while so employed. The female brought very little if any food to the nest until she had finished laying. Apparently neither sex responds to young in the nest during the nest-building stage. Young were introduced into partially built nests in 6 experiments. In 4 of these the owners deserted. In the other two (table 2, experiments 11, 15), the strange nestlings were merely disregarded and became lost or partially buried in the lining as construction proceeded. These observations suggest that sexual activity inhibits the feeding response to nestlings. It should be noted, however, that birds building for the second cycle were simultaneously feeding recently fledged young of the first brood. Tinbergen (1939:45) has noted a similar incompatibility between sexual activity and the response to nestlings in Snow Buntings, and is of the opinion that males of that species may not be able to feed young and pair with a female at the same time. In the domestic chicken, although males do not normally respond to chicks, they may do so following castration.

Observations on feeding-the-young behavior in Tricolored Red-wings may be summarized as follows:

1. Young are fed by adults of both sexes for 11 days in the nest, then for roughly two weeks in the nest vicinity.

2. Feeding responses are aroused by the presence of any nestlings in the "home" nest, and subsequently by fledged young in the nest vicinity. Adults respond to strange nestlings as readily as to their own.

3. The feeding-the-nestlings stage was experimentally reduced to 4 days and extended to 17 days by manipulating nest contents.

4. Feeding-of-nestlings behavior may be discontinued and subsequently resumed during the same breeding cycle.

5. Males respond to young in their own nest at any time after laying has started; females, at any time after incubation has started.

Conclusions.—The development of breeding behavior in the Tricolored Red-wing is closely regulated by physiological factors from the start of nest-building through the initiation of incubation. During the rest of the cycle, however, the rate of development is largely controlled by external situations associated with the nest.

Acknowledgments.—The writer wishes to express his appreciation to Dr. Leon J. Cole of the University of Wisconsin, Dr. Wallace Craig of Albany, N. Y., Dr. Alden H. Miller, Dr. V. S. Asmundson and Dr. Tracy I. Storer of the University of California for many helpful suggestions and criticisms concerning the preparation of this paper.

LITERATURE CITED

Allen, A. A.
1914. The redwing blackbird: a study in the ecology of a cat-tail marsh. Proc. Linn. Soc. New York, 24-25:43-128.
Bissonnette, T. H.
1938. Photoperiodicity in birds. Wilson Bull., 49, (1937): 241-270.
1939. Sexual photoperiodicity in the blue jay, *Cyanocitta cristata*. Wilson Bull., 51:227-232.
Cole, L. J.
1917. Determinate and indeterminate laying cycles in birds. Anat. Rec., 11:504-505.
Cole, L. J., and Kirkpatrick, W. F.
1915. Sex ratios in pigeons, together with observations on the laying, incubation and hatching of the eggs. Rhode Island Agric. Exp. Sta. Bull., 162, 49 pp.
Craig, W.
1911. Oviposition induced by the male in pigeons. Jour. Morph., 22:299-305.
1913. The stimulation and the inhibition of ovulation in birds and mammals. Jour. Animal Behavior, 3:215-221.
1914. Male doves reared in isolation. Jour. Animal Behavior, 4:121-133.
Darling, F. F.
1938. Bird flocks and the breeding cycle (Cambridge Univ. Press), x+124 pp.
Dawson, W. L.
1923. The birds of California (Book-lovers' ed.; San Diego, Los Angeles and San Francisco, South Moulton Co.), 1:104-114.
Friedmann, H.
1934. The instinctive emotional life of birds. The Psychoanalytic Review, 21:1-57.
Goethe, F.
1937. Beobachtungen und Untersuchungen zur Biologie der Silbermöwe (*Larus a. argentatus* Pontopp.) auf der Vogelinsel Memmerstand. Jour. f. Ornith., 85:1-119.
Groebbels, F.
1937. Der Vogel, Bau, Funktion, Lebenserscheinung, Einpassung (Berlin, Gebrüder Borntraeger), 2:xvi+547 pp.
Harper, E. H.
1904. Fertilization and early development of the pigeon's egg. Am. Jour. Anat., 3:349-386.
Herrick, F. H.
1935. Wild birds at home (New York, D. Appleton-Century Co.), xxii+345 pp.
Howard, H. E.
1929. An introduction to the study of bird behavior (Cambridge Univ. Press), xi+136 pp.
1935. The nature of a bird's world (Cambridge Univ. Press), vi+101 pp.

Katz, D.

1937. Animals and men; studies in comparative psychology (London, Longmans, Green & Co.), xi+263 pp.

Kirkman, F. B.

1937. Bird behavior (London, T. Nelson & Sons Ltd.), 232 pp.

1940. Black-headed gull incubating for 75 days. British Birds, 34:22.

Lack, D.

1940. Observations on captive robins. Brit. Birds, 33:262-270.

Lack, D., and Emlen, J. T., Jr.

1939. Observations on breeding behavior in tricolored red-wings. Condor, 41:225-230.

Lashley, K. S.

1915. Notes on the nesting activities of noddy and sooty terns. Carnegie Inst. Washington, publ. 211, Papers Dept. Marine Biol., 7:61-83.

Leverkühn, P.

1891. Fremde Eier im Nest (Berlin, R. Friedländer, etc.), 212 pp.

Manteifel, N.

1937. [Experiments noted] Science, 86, No. 2233, Oct. 15, 1937, supplement, p. 14.

Marshall, F. H. A.

1936. Sexual periodicity and the causes which determine it. Philos. Trans. London, 226B:423-456.

Matthews, L. H.

1939. Visual stimulation and ovulation in pigeons. Proc. Roy. Soc. London, 123B:557-560.

Maxwell, A.

1911. Partridges and partridge manors (London, Adam & Chas. Black), ix+332 pp.

Neff, J. A.

1937. Nesting distribution of the tri-colored red-wing. Condor, 39:61-81.

Patel, M. D.

1936. The physiology of the formation of "pigeon's milk." Physiol. Zool., 9:129-152.

Pearl, R.

1912. The mode of inheritance of fecundity in the domestic fowl. Jour. Exp. Zool., 13:153-268.

Richter, R.

1939. Weitere Beobachtungen an einer gemischten Kolonie von *Larus fuscus graellsi* Brehm und *Larus argentatus* Pontopp. Jour. f. Ornith., 87:75-86.

Riddle, O.

1916. Studies on the physiology of reproduction in birds. 1. The occurrence and measurement of a sudden change in rate of growth of avian ova. Amer. Jour. Physiol., 41:387-396.

1937. Physiological responses to prolactin. Cold Spring Harbor Symposium on Quantitative Biology, 5:218-228.

1938. The changing organism. Carnegie Inst. Washington, publ. 501:259-273.

Riddle, O., and Bates, R. W.

1930. Concerning anterior pituitary hormones. Endocrinology, 17:689-698.

Ruthke, P.

1939. Beobachtungen an Blässhuhn (*Fulica atra* (L.)). Orn. Monatsk., 47:141-147.

Schüz, E. and T.

1932. Brutbeobachtungen am Storch (*Ciconia ciconia*). Beitr. Fortpflanzungsbiologie Vögel, Berlin, 8:18-21.

Skutch, A.

1936. Helpers at the nest. Auk, 52:257-273.

Taibell, A.

1928. Risveglio artificiale di instinti tipicamente femminili nei maschi di taluni uccelli. Atti della Societa dei Naturalisti e Matematici di Modena, ser. 9, 7:93-102.

Tinbergen, N.

1939. The behavior of the snow bunting in spring. Trans. Linn. Soc. New York, 5:1-94.

Watson, J. B.

1908. The behavior of noddy and sooty terns. Carnegie Inst. Washington., publ. 103:187-255.

Witherby, H. F., Jourdain, F. C. R., Ticehurst, N. F., and Tucker, B. W.

1938. The handbook of British birds (London, H. F. & G. Witherby, Ltd.), vol. 1, xl+326 pp.

Whitman, C. O.

1919. The behavior of pigeons (edited by H. A. Carr). Carnegie Inst. Washington, publ. 257, vol. 3:xii+1-161.

Division of Zoology, University of California, Davis, June 23, 1941.