HATCHING BEHAVIOR OF THE BOBWHITE

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THE study of embryonic behavior may contribute greatly to our knowledge of the ontogenetic mechanisms of behavioral development. Synchronization in hatching among certain gallinaceous birds appears to offer a good subject for such study. Vince (1964, 1966) who cites related observations by others, appears to be the first investigator to study the hatching process of the Bobwhite (*Colinus virginianus*) as a coordinated behavioral sequence influenced by environmental factors. She gave special attention to recording the nature of vocal and movement communication and demonstrated that eggs which started incubation 24 hours later than their companions showed a strong tendency to synchronize at hatching time.

The present study was designed to assess the degree of synchronization of hatching of the Bobwhite and to study vocal and movement behavior of incubating embryos as agents in mediating this prehatching synchronization. After the 1964 report by Vince, the plan was enlarged to include observations of the movements of embryos through windows in the shell; and also, to test eggs delayed in incubation 48 hours after that of their companions. The terms "pipping stage," "clicking stage," and "chipping stage" used to denote successive behavioral phases of the total hatching process differ from those used by Vince only for the last phase. In this study the term "chipping stage" is used since Vince's term "hatching stage" seems more appropriately applied to the total process and "chipping stage" denotes that last phase of hatching beginning with the onset of the "surge-pip" behavior resulting in the removal of the shell fragments while turning in the egg and final emergence.

METHODS

Eggs from breeding birds housed in outdoor cages were incubated under bantam hens for 21 or 22 days until the advanced eggs (those placed in incubation one or two days before their delayed companions) began to pip. At this stage all eggs were transferred to the observation incubator operated at a temperature of 101–102 F (except one test observed at 95–98 F). Twelve hatchings were recorded during the seasons of 1965 and 1966 as outlined in Table 1. Segregated eggs were placed in small padded trays apart from larger trays containing clutches (Fig. 1). Successive hatchings were kept under continuous observation throughout day and night. A stop watch was used to record intervals between rhythmic pipping movements of the "chipping stage" (behavior consisting of successive "surge-pip" movements). The behavioral movements of the prehatched bird during the chipping movements phase of hatching were studied as follows: A. After these movements started,

TABLE 1
INCUBATION PLAN AND HATCHING DATA

Tests		Eggs pipped	Test plan	Number hatched	Stage at death	Average incubation time	Spread in hours
1965	1966						
1		5	all in clutch	5		561.6	2
1a		6	clutch	5		577.0	3
	1b	8	clutch	6	pipped	601.0	6
	1c	5	clutch	3	clicking	585.0	1
2		6	single egg segregated	3	clicking		22
	2a	5	single egg segregated	2	clicking	600.2	26.5
3		12	in pairs, one 24 hours delayed*	3 early 6 delayed	clicking	572.7 551.8	3.5 3.1
4		24	in pairs, one 48 hours delayed*	10 early 8 delayed#		558.8 528.8	30 43
		5	control group in clutch delayed date	5		561.5	2
5		11	one clutch				
			5 advanced	5 early		571.8	3.7
			6 delayed 48 hours	5 delayed		524.3	0.5
	5a	20	one clutch				
			9 early	7 early			1.0
			11 delayed 48 hours	11 delayed			6.8
	5b	16	one clutch				
			5 early			585.5	1.0
			11 delayed (temp. 95–98 F) 48 hours			587.0	3.3

* Eggs started incubation 24 or 48 hours later than their "early" companions.
\# *T* is significant beyond 0.01 level in Wilcoxon matched-pairs signed rank test.

parts of the shell around the beak and head were removed to facilitate observations of the head movements and responses (Craig, 1912); B., egg caps were detached to be set out slightly from the main body of the egg where they were secured in place by narrow strips of tape in a manner to allow the rotating embryo freedom to continue without having the egg tooth contact the shell or shell membrane; and C., using preparations described above, four eggs were further treated by extending first one and then both feet

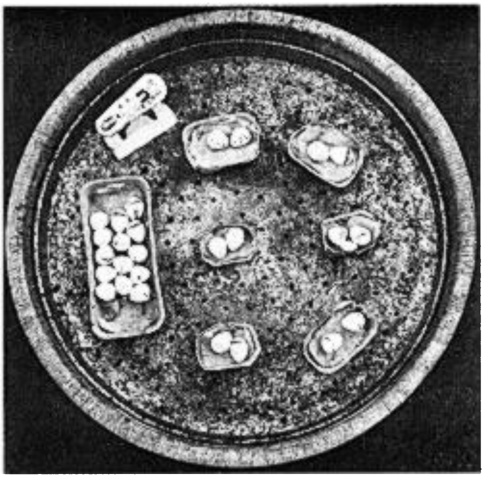

FIG. 1. Showing observation incubator with eggs hatched in a clutch in the large tray, and eggs in pairs (one advanced and one delayed) in each small tray.

through a window in the small end of the shell. Thus, analysis of the rhythmic movements of feet, body and head were observed.

RESULTS

In tests 1, 1*a*, 1*b*, and 1*c* where eggs were hatched in clutches simulating natural conditions, the average incubation time for the four clutches varied from 561 hours to 601 hours, but the spread between the first and last egg to hatch of any one clutch was only six hours, usually much less (Table 1). This high degree of synchronization is a result agreeing with that reported by Vince.

In tests 2 and 2*a* where eggs were hatched in isolation after pipping, the data are too meager to be more than suggestive. The few chicks that did hatch in these tests came out over a long period of time (22 hours to 26.5 hours). The number of deaths in the pipped and clicking stages, after isolation in the early pipped stage, was high. This tendency continued among the advanced eggs matched with 24 hour delayed eggs. Vince apparently did not get this result. She, referring to eggs kept in isolation says (1966), "these eggs all hatched normally but, if the embryos stimulate each other the development of isolated eggs could differ from that of eggs hatched in clutches."

In test 3 where 12 eggs isolated in pairs with one of each pair 24 hours delayed at the beginning of incubation, half of the early eggs died in the clicking stage. Those that hatched required an average of 572.7 hours incubation time whereas the six delayed companions, one of each pair, all hatched in an average of 551.8 hours, and the average of the hatching time for the delayed eggs was only 3.1 hours behind that of the early companions.

In test 4 where 29 eggs were placed in the incubator, 24 were arranged in isolated pairs so that one of each pair started incubation 48 hours later than its companion. Five eggs started on the delayed date were retained together in a clutch as a control group. The hatching data show synchronization with the delayed eggs of isolated pairs brought forward in their hatching time. Results show 528.8 hours average for the delayed eggs compared to 558.8 hours for the advanced companions; whereas, the control clutch of delayed eggs was comparable in total hatching time to the average for the advance members of the isolated pairs. The Wilcoxon matched-pairs signed rank test shows the delayed birds have a speeded incubation period. The results gave * T significant beyond 0.01 level. Applying the T-test to the same data, the result * T is significant beyond the 0.001 level.

In tests 5 and 5*a*, eggs were hatched in clutches with a part of each clutch delayed 48 hours. A marked degree of advancement in the hatching time for the delayed eggs is shown in each test. In test 5b where 16 pipped eggs were incubated at a temperature of 95–98 F, eleven of which were 48 hours delayed and kept continuously with the five advanced companions in one clutch no synchronization occurred between the early and the late ones. But those of each incubation date synchronized within their group. The average for the early was 585.5 hours and for the delayed 587.0 hours.

DISCUSSION

In all eggs placed in incubation either 24 or 48 hours after their companions and transferred from bantams to an observation incubator operated at 101–102 F, the delayed eggs showed a tendency to advance their hatching and to synchronize with their earlier companions. Vince (1964) obtained this result for eggs delayed 24 hours but she did not report trials with the longer 48 hour delay period. Records of the time spent in the three hatching stages—pipping, clicking, and chipping, indicate that the greatest degree of stimulation of delayed embryos came during the clicking of their early companions. Vince (1966) has shown that there is vocal sound and movement with rhythmic sequence during all stages of hatching and that its expression is strong and rhythmically regular in the last two phases of hatching.

The third behavioral phase in hatching, which I have called "chipping stage," is made up of a series of spasmodic muscular movements involving the leg, trunk, and head muscles. Each "surge-pip" begins with the leg push and progresses through the trunk region ending with a strong downward tipping of the head after the upper thrust which pushes the egg tooth through the shell. This movement, like clicking, is rhythmic in operation. Each new "surge-pip"

TABLE 2
HATCHING DATA (SAMPLE)

Egg mark	Incubation status	Hours pipped	Hours clicking	Minutes chipping	Number of rotations in shell	Intervals in seconds between "surge-pip" movements
A^2	advanced	33	12.25	17/60	2.25	7-6-7-7-7-7-7-7-7-7
N^2	delayed	*		25/60	1.0	5-4-7-4-5-5-6-6-6-7-7-5-5-5-5-5-5-5-5-7-5-6
K^2	delayed	13	19	20/60	1.75	4-4-4-4-5-5-5
G^2	delayed	9	2.5	15/60	1.50	8-6-7-9-6-6-1-9-8-7
Q	delayed		15.0	33/60	3.50	7-15-10-13-5-5-5-6-6-5
L^2	delayed		17.0	30/60	1.75	8-6-7-8-4-8-3-5-7-3-6-7-6-7-6-7
O^2	delayed			20/60	2.50	8-8-8-8-7-8-8-4
H^2	advanced	27	11.0			6-6-7-67-7-8-6-5
D	advanced	20	17.0	20/60	3.50	
E	advanced	20	9.6	20/60	2.50	
H^3	delayed	8	10.75	30/60	6.50	
E^2	delayed	16	11.0	45/60	6.40	
G	delayed	29	11.50	27/60	2.50	
I	advanced	15	9.0	18/60	3.50	

* Data not recorded.

movement comes generally after six, seven, or eight second intervals (Table 2).

The final triggering of the "surge-pip" movements ending the chipping stage appears to be the infectious factor in starting the same advancement in adjacent eggs. Thus, we may hypothesize that there are two levels of stimulation of delayed embryos influenced through sound and movement communication and that activity characteristic of the clicking stage stimulates delayed embryos to act earlier than they would otherwise, and that the first embryo of the clutch which begins to "surge-pip," jarring its companions, stimulates them to begin similar action. Embryos may have been in the clicking stage for hours, yet when one in a clutch of eggs begins the "surge-pip" effort, they usually all soon begin, and then emerge within 20 to 30 minutes.

Clicking begins slowly and works up to a crescendo. Vince (1966) has shown that it develops independent of lung ventilation and breathing. One might expect a time requirement for its maturation, yet some of the delayed eggs in the 48 hour delay test completed all three of the hatching phases in about 4 hours. Other advanced eggs remained in the clicking stage for 26 hours.

In test 5*b* where there was no ill effect on the quantity of hatch at the lowered temperature, and no synchronization between early and late eggs we may find a suggestion for exploring operational thresholds of stimulation

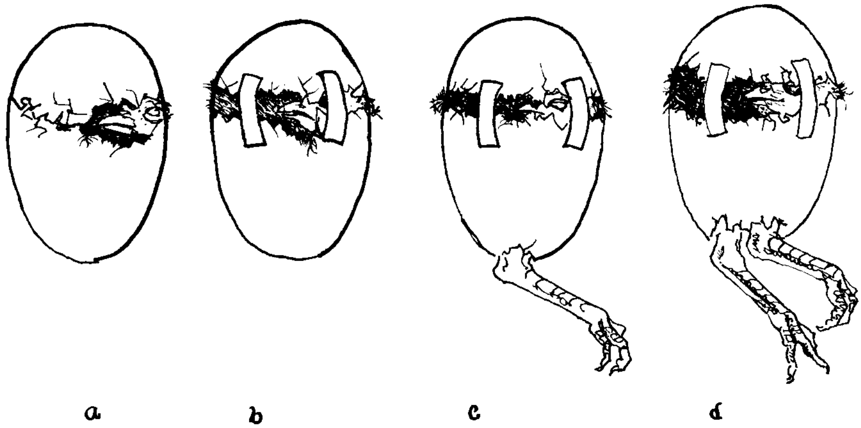

FIG. 2. Showing method of preparing eggs for observation of prehatching behavior.

factors; but, further investigation of the role of temperature levels is needed.

The feet and neck of the quail chick are proportionally longer than those of domestic chickens and occupy relatively different positions within the shell. In the Bobwhite chick the left leg lies with the heel against the small end of the shell but the long tarso-metatarsus extends ventrally and upward to bring the toes near the pipping location. The right foot lies more to one side with the toes folded back of the wing. Observations made through a shell opening made by extending the egg cap (Fig. 2b), indicated at first, that the left leg and foot might be responsible for the chicks rotary movement within the shell. But, when the small end of the shell was removed and the left leg extended outside the egg (Fig. 2c) the "surge-pip" continued as before, although at first the rotary progress stopped. After a few minutes that progress was resumed at a slower than normal rate. Following this discovery the right foot was also extended from the shell (Fig. 2d) which did not effect further change in behavior or progress. With the cap of the shell extended so that the egg tooth made no contact with the shell, the entire rhythmic movement of the "surge-pip" action became clear. Each effort began with a strong push on the left heel and foot attended by a weak scratching movement with the right foot. Then trunk muscles expanded with inhalation which exerted strong pressure on the upper curvature of the shell in the region of the lower cervicals. While this pressure was being applied the head made a strong tip-up movement causing the tooth to penetrate the shell. Then suddenly, all pressure was relaxed except the contact of the skull against the shell. The last component of this coordinated "surge-pip" action was a deep strong depressing movement of the beak which because of contact of the top of the head and the hatching muscle with the shell (Fisher, 1958) gripped the shell sufficiently to rotate it a small distance in a counter-clockwise direction. Thus, when the next "surge-pip" seizure occurred, 6 to 8 seconds later, a new advanced location on the shell was pierced. Any slight amount of drying of the pierced membrane caused it to shrink, which slowed or stopped the rotary advancement of the hatching process. In these cases, "surge-pip" movements continued for some time although death in the shell was imminent. Under normal conditions strong embryos leave unpierced spaces in the shell membrane as they progress with one "surge-pip" movement after another, and these may require from three to six rotations within the shell to cut the egg cap free and allow the chick to emerge. Ordinarily, two or three times around frees the cap and allows the bird's head to extend free. As soon as the neck straightens from its coiled position within the egg all "surge-pip" movements cease.

It may be significant to note that these "surge-pip" efforts are actually a series of coordinated movements which originate in the caudal region of the embryo and advance to the head region. This appears to be a development which was not seen by Kuo (1932) for domestic chickens. He states, "The development of embryonic behavior in the chick begins from the head and progresses caudal. Every embryonic movement, after its first appearance, tends to persist throughout embryonic life or even after hatching, unless it is interfered with, or modified by, structural or environmental changes."

SUMMARY

Eggs from Bobwhite in incubation tests at 101–102 F indicated synchronization at hatching when placed in clutches and/or segregated pairs with 24 or 48 hour delay periods for matched eggs. One test at temperature 95–98 F and 48 hour delay period failed to show these results. Statistical treatment in the case of test number 4 (matched pairs with one 48 hours delayed) is given and showed T significant beyond 0.01 level in the Wilcoxon matched-pairs signed rank test.

The behavioral characteristics of three phases of hatching are discussed and the term "chipping stage" is used to denote the last of these successive stages. The term "surge-pip" is given to the rhythmic behavior repeated during the chipping stage. Elements of this behavior are discussed in relation to the anatomical parts involved and the events leading to the chick's emergence.

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JOSSELYN VAN TYNE AWARD

A sum of $1,194.82 is available in the Josselyn Van Tyne Memorial Fund for research grants in 1969. Of this amount, $185.00 is earmarked for research in systematics. Any student of birds is invited to apply for research grants. Young men and women just starting their careers or others not eligible for government grants are encouraged to apply.

Applicants should prepare a brief but comprehensive description of their research projects specifying the objectives and proposed plans of procedure. Particulars of the type and amount of financial assistance needed must be included. A brief statement of the applicant's ornithological background should be appended. Letters of recommendation from one or more recognized ornithologists would be helpful.

Applications should be submitted not later than 1 April 1969 to the Chairman of the A.O.U. Research Committee, Dr. Richard C. Banks, Bird and Mammal Laboratories, U. S. National Museum, Washington, D. C. 20560.