

Hatching behavior of the chick (*Gallus domesticus*): Plasticity of the rotatory component*

ROBERT R. PROVINE†
Washington University, St. Louis, Mo. 63130

The plasticity of the rotatory component of hatching behavior was tested by taping down the shell cap in order to prevent hatching. It was found that embryos with taped shells rotate farther than do untaped controls. The adaptive and comparative significance of this finding is discussed.

A detailed study of the hatching behavior of the chick embryo by Hamburger & Oppenheim (1967) has indicated that, on about Day 17, smooth and apparently coordinated prehatching movements (Type III) appear among the jerky, apparently uncoordinated movements (Types I and II), which were present up to this time (Hamburger, 1963). These prehatching movements include: the lifting of the head out of the yolk sac; the tucking of the head under the right wing; penetration of the membrane separating the embryo from the air chamber; and pipping (cracking a hole in the shell). The shell is opened by back thrusts of the head and beak against the shell. On Day 21, the chick gains exit from the shell by continuing the back thrusts while performing rotatory movements in a counterclockwise direction, as viewed from the blunt end of the egg. When the shell has been cracked around approximately two-thirds of its circumference, the shell cap breaks off and the chick emerges.

In the present experiment, the plasticity of the important rotatory component of hatching behavior is tested by taping down shell caps in order to prevent hatching. The amount of rotation of embryos with taped shells is compared with that of untaped controls. The outcome should indicate whether the angular distance that embryos rotate in hatching is modifiable or a rigid component of a fixed action pattern.

METHODS

Embryos were raised from fertile eggs of a Kimber strain, Flock K137. The eggs were incubated in a forced draft incubator that was maintained at

37° C and 70% relative humidity. The eggs were turned several times a day. On the 19th day of incubation, embryos were transferred to another incubator and were no longer turned. Only those embryos pipping at the blunt end of the shell were used in the study.

When an embryo pipped, a line was drawn from the pip hole to the blunt pole of the egg. This was the zero point for the study of rotation. Shell caps were secured by two perpendicular strips of 6-mm masking tape, which were wrapped around the egg from pole to pole. Care was taken not to obstruct the pip hole. Experimental embryos were observed at intervals that ranged from 15 min to 1 h during daily 8-h observing sessions. The intervals between observation periods were not critical because the variable being measured was the total amount of rotation. During each observation period, the position of the beak's tip was marked on the shell and notes were taken concerning the behavior of individual embryos. If 2 consecutive days had passed with no

rotatory progress being made, an embryo was removed from the incubator and the farthest excursion of the beak's tip was marked on the shell and measured in terms of the total angular travel from the original pip hole. These measurements were made with a protractor device. Control embryos were continuously observed during the final stage of hatching or climax (Hamburger & Oppenheim, 1967). Control embryos were allowed to hatch normally. The farthest angular excursion of their beak tips from the original pip hole, before hatching, was measured. Eighty control and 80 experimental embryos were used (total N = 160).

RESULTS

Figure 1 shows the amount of rotation of control (normal shells) and experimental (taped shells) embryos. The embryos with taped shells rotated an average of 440.29 ± 164.42 deg (SD) vs 243.52 ± 56.83 deg for controls. These differences were highly significant ($t = 10.05$, $df = 158$, $p < .001$). The much greater amount of rotation shown by the experimental embryos indicates that all embryos have the capacity for sustained rotation. This capacity may be demonstrated under certain conditions, such as those of the present study. Under normal conditions, the capacity for sustained rotation is not fully exercised because rotation is curtailed by hatching. These findings further indicate that the amount of rotation shown by a given chick population is only relative, being influenced by factors affecting the difficulty encountered in escaping from the shell. Therefore, the amount of rotation reported for the control

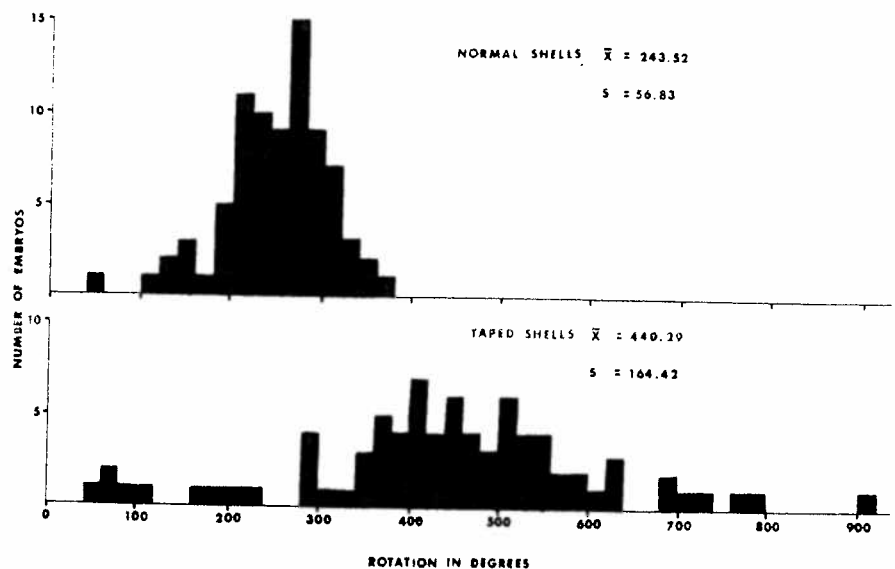


Fig. 1. The numbers of embryos with normal (untaped) and taped shells which showed different amounts of rotation.

*I thank Dr. Viktor Hamburger and Dr. R. W. Oppenheim for their helpful comments. An abstract of this study appeared in *American Zoologist*, 1971, 11, 620. The work was supported by USPHS Grant 1900 and traineeship under Grant P10 ES 00139 through the Center for the Biology of Natural Systems, Washington University.

†Present address: Department of Biology, Washington University, St. Louis, Mo. 63130.

embryos in the present study should be considered as an approximate value.

In all cases, hatching movements were executed with considerable vigor. This was particularly evident in several experimental embryos that managed to escape from taped shells. This was accomplished by violent kicking and struggling, which completely shattered the shells, allowing the chicks to exit between the tape strips on the sides of the shell. Likewise, several control embryos that failed to break off their shell caps hatched by breaking out of the sides of the shell.

DISCUSSION

The present investigation indicates that the chick has evolved a highly adaptive behavior that maximizes the probability of hatching under a wide variety of environmental conditions. The capacity for sustained rotation increases the likelihood that the embryo will crack enough of the shell's circumference to permit hatching. The amount of rotation exercised by a given embryo is dependent upon the difficulty it encounters in gaining release from the shell.

The present finding that the amount of rotation may be increased in the taped shell condition agrees with the observation made by Corner & Bakhuis (1969), that the stereotyped bursts of struggling associated with rotation and hatching may be extended by up to 5 to 7 h if chicks are prevented from escaping from their shells. (The method used for restraint and the effect of sustained struggling on the amount of rotation was not mentioned by these investigators.) It seems reasonable to predict that this sustained struggling would result in extended rotation. Corner and Bakhuis also performed the converse of the above experiment, which involved the artificial and premature release of chicks from their shells. Embryos that were prematurely released terminated the struggling movements, even if they had just been initiated. These investigators concluded that stretching of the neck, which occurs after escape from the shell, is responsible for terminating the hatching movements.

A mechanism that may be involved in rotation was proposed by Kovach (1970). He observed that the alternating leg movements, which are crucial to rotation (Hamburger & Oppenheim, 1967; Oppenheim & Narayanan, 1968; Helfenstein & Narayanan, 1969) resemble a postural reflex component of righting behavior, which is observed after hatching. On the basis of this descriptive evidence, he proposed that righting reflex activity may be involved in rotatory behavior. The present data and the previously described results of Corner & Bakhuis (1969) offer some support for this proposal. If a component of the righting reflex is involved in rotation, we would predict the present finding that rotation is maintained in the taped shell condition because the stimulus environment responsible for evoking and maintaining the behavior would remain constant.

If the present findings are considered in light of the observation that rotatory climax movements appear *de novo* shortly before hatching (Hamburger & Oppenheim, 1967), a view of rotatory behavior emerges that incorporates both endogenous and environmental factors. Rotatory movements may be initiated by internal physiological processes, possibly humoral or neural in nature (Oppenheim, in press, b), but these movements may be dependent upon the environmental conditions associated with constraint for their performance and maintenance. When the chick loosens its shell cap and escapes from the shell, it is released from constraint. This would serve to remove the stimulus required for rotation, if reflex activity is involved, or turn off an ongoing endogenous pattern of rotatory movements. In any case, the rotatory behavior would be conveniently terminated when its utility was exhausted.

The present findings are interesting from a comparative point of view because they offer a possible explanation of the varying amounts of rotation observed in different species of birds. If the amount of rotation is a function of the difficulty in escaping

from the shell, we may expect embryos with thin shells to show little rotation and embryos with more challenging hatching tasks to show more rotation. This proposal has some support. Gulls, which have relatively thin shells (Fisher, 1966), rotate only 65 deg, while quails, which have thick shell membranes (Romanoff & Romanoff, 1949), rotate an average of 528 deg before hatching (Oppenheim, in press, a, b). This suggests that diverse species of birds may possess similar rotatory capabilities and mechanisms, but that they vary in regard to rotatory performance.

REFERENCES

- CORNER, M. A., & BAKHUIS, W. L. Developmental patterns in the central nervous system of birds. V. Cerebral electrical activity, fore-brain functions and behavior in the chick at the time of hatching. *Brain Research*, 1969, 13, 541-555.
- FISHER, H. I. Hatching and the hatching muscle in some North American ducks. *Transactions of the Illinois Academy of Science*, 1966, 59, 305-325.
- HAMBURGER, V. Some aspects of the embryology of behavior. *Quarterly Review of Biology*, 1963, 38, 342-365.
- HAMBURGER, V., & OPPENHEIM, R. W. Prehatching motility and hatching behavior in the chick. *Journal of Experimental Zoology*, 1967, 166, 171-204.
- HELFFENSTEIN, M., & NARAYANAN, C. H. Effects of bilateral limb-bud extirpation on motility and prehatching behavior in the chick. *Journal of Experimental Zoology*, 1969, 172, 233-244.
- KOVACH, J. K. Development and mechanisms of behavior in the chick embryo during the last five days of incubation. *Journal of Comparative & Physiological Psychology*, 1970, 73, 392-406.
- OPPENHEIM, R. W. Prehatching and hatching behavior in birds: A comparative study of altricial and precocial species. *Animal Behaviour*, in press, a.
- OPPENHEIM, R. W. Prehatching and hatching behavior: A comparative and physiological consideration. In G. Gottlieb (Ed.), *Prenatal ontogeny of behavior and the nervous system*. Chicago: University of Chicago Press, in press, b.
- OPPENHEIM, R. W., & NARAYANAN, C. H. Experimental studies on the hatching behavior in the chick: Thoracic spinal gaps. *Journal of Experimental Zoology*, 1968, 168, 387-394.
- ROMANOFF, A. L., & ROMANOFF, A. J. *The avian egg*. New York: Wiley, 1949.