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AVIAN PREHATCHING BEHAVIOR: FUNCTIONAL ASPECTS OF THE TUCKING PATTERN

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The domestic chick's position at the time of pipping (initial cracking of the eggshell) is important to its hatching success. Normally the anterior end of the chick is at the large end of the egg; the legs, feet, and left wing are flexed; the neck is depressed ventrally; the head is turned to the right, its left side resting on the right pectoral muscle, and is tucked under the partially extended right wing (Fig. 1a). Six "malpositions" generally reducing hatchability have been recognized by poultry scientists. Malposition VI, head over the right wing (Fig. 1b), reduces hatching, but so slightly that Waters (1935), Byerly and Olsen (1937), Munday (1953) and others did not consider this position abnormal.

Hamburger and Oppenheim (1967) detailed the specific prehatching pattern of "tucking," the placing of the head under the right wing 1-2 days before pipping. This attitude is maintained throughout the hatching "climax" stage of cutting the cap from the shell. It is a genetically consistent behavior pattern of the chick and probably of most birds (see Oppenheim 1972). Thus I was interested to learn that its absence (producing malposition VI) does not seriously hamper pipping or hatching. This could be explained by the fact that only a very slight selective advantage is necessary to fix an adaptation in a species over a large number of generations, but it still remains to elucidate the function(s) of the wing and the actual selective advantage produced by tucking.

What is the function of the normal wing-over-head position? Kuo's (1932) supposition that it is important for the wing to protect the face from the air chamber membrane has been shown invalid by Waters (1935) and Hamburger and Oppenheim (1967). Protection of the head or eyes from sharp shell fragments during the head thrusts of climax could be a function, but the eyes generally remain closed until hatching is completed in precocial birds (Hamburger and Oppenheim 1967), longer in altricial birds, and the eyes may need no extra protection. Also, Oppenheim (1972) stated that the wing in altricial birds does not cover much of the relatively large head. Normal pipping convulsions (Brooks and Garrett 1970) might deform the delicate wing bones if the wing were between thorax and beak in malposition VI. Wing protection is not needed in the hatching climax, however: the thorax does not push against the beak, now, because there is sufficient space in which to elevate the head; and the force does not have to be as great to break the eggshell (which is already broken) further. Yet the wing covers the head throughout. Narayanan and Oppenheim (1968) hypothesized that tucking inhibits head movements. In their experiments involving extirpation of the right wing bud, a significant increase in frequency of head

movements was demonstrated, but the cause of the increase was obscured by possible neural modifications due to limb extirpation. Later Oppenheim (1970) re-tested this by manually "un-tucking" chicks and ducklings, but no significant increase in frequency of head movements was shown this time. In any case, it seems doubtful that a decrease in frequency (rather than amplitude) of head movements would produce the selective pressure necessary to evolve the tucking pattern. In fact, the opposite might be more beneficial.

In normally positioned chicks, an orifice formed by the extended right humerus and the flexed right femur or the knee encloses the beak (Fig. 1a). I propose that this "hatching orifice" functions primarily as another of several mechanisms (see Brooks and Garrett 1970) to keep the beak tip in place during pipping. Thus, force is applied successively at the same location on the shell, in order to break through it with less total effort. In malposition VI the orifice disappears (Fig. 1b) and the tip is free to move anteriorly (but not posteriorly, due to the knee).

It is also probable that tucking is of some value in climax. Réaumur (1751, in Hutt 1929) was the first to suggest, and probably correctly so, that the wing-over-head position is useful in climax to keep head thrusts aimed properly. Bakhuis (1974) showed that both wings aid in the chick's rotation during climax. If the right wing were not over the head it could not function in this capacity.

METHODS

To ascertain whether the wing requires protection during pipping I placed White Leghorn Chicken (*Gallus gallus*) eggs in a standard cabinet incubator for 19-20 days. A few hours before predicted pipping time, windows were placed in nine eggs (method of Brooks and Garrett 1970) and each chick was manually "un-tucked." They were observed until pipping and the right wing was examined closely for damage.

To test relative amplitude of anterior head movement with and without the presence of the hatching orifice, windows were placed in 27 newly pipped eggs (size of opening ca. 4×2.5 cm). The chicks were manually un-tucked and rotated so that the beak tip lightly touched a 5×3 cm thin glass coverslip sealed to the eggshell with modelling clay and firmly secured with cellophane tape. Thirty controls were treated similarly except that they were not un-tucked. The location of the beak tip was observed continuously and marked on the glass for an average of 13.3 h (range, 1.5-25 h) with un-tucked chicks, and 12.3 h (1.5-29 h) with controls. A few chicks that re-tucked themselves were again un-tucked. When a chick rotated in the shell, beginning climax, observation ceased.

RESULTS AND DISCUSSION

The wing-damage hypothesis was discounted when no damage was noted in any chick's right wing.

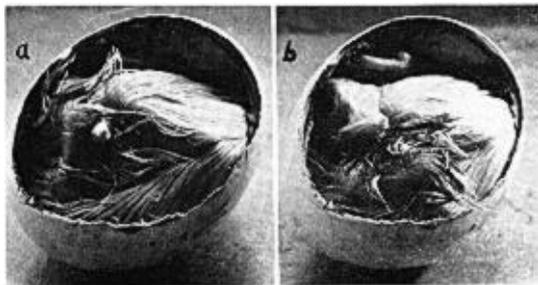


FIGURE 1. Normal pipping position of chick, showing right wing over head to form hatching orifice (a). The same chick placed in malposition VI, showing disappearance of hatching orifice (b).

However, in the amplitude testing, experimental chicks' beak tips moved a maximum (mean \pm SD) 14.33 ± 6.15 mm (range, 3–28 mm), and control chicks' only 7.87 ± 3.14 mm (3–15 mm), a significant difference (F-test, $P < .05$). An average increase of 82% in anterior beak tip displacement was promoted by malposition VI, supporting the hypothesis that tucking reduces prehatching head mobility.

If the beak is not in the hatching orifice, the force of successive pipping convulsions may not concentrate locally. The potential for anterior movement thus should result in pipping being retarded or precluded at times, and the pip should average closer to the large end of the egg. An attempt to assess retardation of pipping by determining whether re-pipping was delayed or precluded in un-tucked chicks manually rotated away from the original pip was unsuccessful. Three experimental chicks and two controls did not re-pip, and very wide variation in re-pipping times for 17 controls (2–1418 min) and 18 experimentals (25–1020 min) afforded no valid statistical comparison. Significantly, though, Hutt and Pilkey (1934) noted that pipping movements were ill-directed and that pips often were closer than normal to the large end of the egg for chicks in malposition VI.

Bakhuis (1974) showed that during the short, intense bursts of climax activity both wings (and both legs) were extended and pressed against the shell. At the beginning of a burst he felt that the wings and other body parts prevented a clockwise rotation of the chick that otherwise would occur due to simultaneous strong pressure of the beak against the shell. However, I do not agree that pressure from the *right* wing is effective, here, because the beak is exerting pressure at a point on the eggshell very near and on the same side as the wing. Pressure from extension of the right wing, in fact, could well be counterproductive at this time. Bakhuis also determined that near the end of a climax burst, when beak pressure on the shell was relieved, the wings and certain other members were responsible for the counterclockwise rotation of the chick necessary to continue cutting the egg cap. In this case the right wing probably would be operative. Tucking, therefore, seems to have importance in climax, since it would be impossible for this wing to exert the proper pressure if it were lodged under the head. This particular action of the right wing would be counterproductive in pipping, however, because a minimum of rotation is desirable at this time, so that beak pressure can occur at the same place on the shell several times in succession. Therefore, the wing may not extend during this phase of

hatching (Bakhuis did not examine pipping movements).

If the right wing's pressure is either minimally effective or is nonexistent in pipping, as seems to be the case, malposition VI should not disrupt this phase of hatching. Yet we know from the observations of Hutt and Pilkey (1934) that it *is* somewhat disruptive. This indicates that tucking occurs prior to pipping for reasons other than to produce pressure by the right wing on the eggshell. If tucking were not operative in pipping itself, the question would arise as to why this behavior pattern occurs well before pipping begins. To reduce anterior mobility of the beak seems to be the likely answer.

Tucking behavior appears to have one plausible function in pipping, and probably two in climax (remember Réaumur's common-sense suggestion concerning the wing's aid in aiming head thrusts during climax). Because the temporary opening that encloses the beak is probably used in both phases of hatching, the term "hatching orifice" is deemed most appropriate for this "structure" that is produced by tucking.

With the beak tip localized on the shell in part by the hatching orifice, both the chances and speed of pipping are increased, especially the latter. Cutting the shell in climax would be surer and quicker in the tucked position. Lower energy expenditure due to fewer wasted motions thus should occur in both stages of hatching, and this may be the selective advantage of tucking. It would appear to have posthatching selective value in wild birds: a hatchling that is less fatigued or has more reserve energy upon hatching should be able to compete better with siblings, and if precocial, should gain locomotory function earlier. Another aspect involves the click-communication known to synchronize a brood's hatching (Vince 1969) in many species. This is probably explained in precocial birds by the predatory penalty exacted upon a brood that remains in the nest too long after hatching. If hatching of an individual is delayed too long or is too strenuous, the late hatcher or weakened hatchling may well be abandoned, the earlier chicks already having vacated the nest with the parent because of genetic selection against paying that predatory penalty.

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EFFECT OF A NEW TRANSMISSION LINE ON WINTERING PRAIRIE RAPTORS

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Most birds of prey hunt from a perch that provides a commanding view of the hunting area (Brown and Amadon, p. 70-71, Eagles, hawks, and falcons of the world, McGraw-Hill, New York, 1968). Hillsides, rocky outcrops, and trees along streams provided perches on the Great Plains before the arrival of modern man. Man has erected many structures, particularly fenceposts, power poles, and windmills, that have subsequently been used as perches by prairie raptors. Marion and Ryder (*Condor* 77:350-352, 1975) found that Golden Eagles (*Aquila chrysaetos*), Rough-legged Hawks (*Buteo lagopus*), and Prairie Falcons (*Falco mexicanus*) preferred higher man-made perches. As part of a study of the effects of a new 230 kV transmission line on prairie wildlife, I counted raptors along its right-of-way during the winters of 1973-74 (before construction) and 1974-75 (after construction). This note reports the effect that this new line had on the local distribution and numbers of wintering diurnal raptors.

STUDY AREA AND METHODS

The transmission line, which dominates the prairie skyline, extends 125 km from the Midway Substation, 32 km S of Colorado Springs, Colorado, across gently rolling terrain to the Big Sandy Substation, 4 km NE of Limon, Colorado. Wooden H-frame towers which are 23 m high support three conductors and two overhead ground wires. Shortgrass prairie, dominated by blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*), occurs along 70 km (56%) of the line. Sandhill prairie, predominately sandhill bluestem (*Andropogon hallii*), and sandreed (*Calamovilfa longifolia*), occupies 29 km (23%) of the line, while cropland, primarily winter wheat (*Triticum anetivum*), underlies 25 km (20%) of the line. One km (1%) of the line crosses the predominately cottonwood (*Populus sargentii*) flood plain of Fountain Creek, the area's only permanent stream.

I counted raptors along 80 km of the line, primarily in shortgrass and sandhill prairie, approximately every two weeks between mid-November and mid-March each year. Most of the census route was on county and primitive roads near the powerline right-of-way (ROW) because fencelines impeded ROW travel before access gates were built. Each count began within an hour after sunrise and continued

TABLE 1. Proportional use of perch types by diurnal raptors observed *beyond* 0.4 km of the transmission line during winter censuses before and after construction.

Species	Time period	No. perched	Proportion of perched raptors on				
			REA pole	Fence-post	Tree	Wind-mill	Other
Rough-legged Hawk	before	15 (15) ¹	.60	.20	.00	.07	.13
	after	19 (23)	.53	.10	.16	.16	.05
Golden Eagle	before	12 (15)	.33	.25	.08	.25	.08
	after	10 (15)	.20	.40	.20	.10	.10
Prairie Falcon	before	3 (4)	.67	.33	.00	.00	.00
	after	5 (6)	.80	.20	.00	.00	.00
All raptors ²	before	39 (53)	.44	.26	.10	.10	.10
	after	48 (71)	.42	.25	.15	.10	.08

¹ Number seen.

² Includes nine species.