ONSET OF INCUBATION IN YELLOW WARBLERS: A TEST OF THE HORMONAL HYPOTHESIS

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ABSTRACT.—Mead and Morton (1985) suggested that asynchronous hatching for birds in which only the female incubates is caused by a hormonal surge associated with the ovulation of the last ovum. This hormonal surge is believed to inhibit further ovulation and simultaneously stimulate females to initiate full incubation. Thus, the advantages, if any, accrued from asynchronous hatching are merely epiphenomena. The hormonal hypothesis predicts that regardless of clutch size, full incubation is initiated with the laying of the penultimate egg. We also predict from the hypothesis that incubation attentiveness during egg laying will be similar in females tending either four- or five-egg clutches, especially on the day the penultimate and last eggs are laid, hatch spreads will be similar in four- and five-egg clutches, and the addition of eggs during egg laying will not induce increased incubation attentiveness. In a three-year study (1988–1990) on Yellow Warblers (*Dendroica petechia*) nesting at Delta Marsh, Manitoba, we found that incubation attentiveness during egg laying was similar between females that produced four- and five-egg clutches, but full incubation was not initiated prior to the last egg being laid. Despite apparently similar incubation attentiveness during egg laying, hatch spreads differed significantly between four- and five-egg clutches. Incubation attentiveness was increased experimentally by adding eggs during early egg laying. We suggest that initiation of full incubation is not rigidly controlled by hormonal changes associated with the laying of the penultimate egg. Therefore, asynchronous hatching of the penultimate and, especially, the last egg does not require full incubation. *Received 16 January 1991, accepted 8 November 1991.*

IN MOST bird species, successful incubation requires the development of one or more brood patches on the abdominal surface of the incubating bird. Brood patches often are free of feathers, are oedematous, and have highly vascularized skin that enhances heat transfer (Pettingill 1985). Brood-patch development involves both defeatherization and vascularization (Drent 1975), which are regulated by prolactin in concert with estrogen (e.g. Bailey 1952, Hinde et al. 1963, Selander and Kuich 1963, Lloyd 1965, Jones et al. 1970). Vascularization is generally completed prior to egg laying (Bailey 1952, Brackbill 1958, see also references in Drent 1975) and defeatherization occurs at least by early incubation (Haftorn 1981, see review in Drent 1975). Therefore, incubation behavior, which is stimulated and/or maintained by stimuli arising when the brood patch is in contact with the eggs (White and Kinney 1974, Hall and Goldsmith 1983), can be and is effective even during laying (Haftorn 1978, Zerba and Morton 1983).

Although prolactin may not initiate incubation behavior, there is evidence that incubation is maintained by it (Drent 1975). The secretion of prolactin is apparently stimulated by the act of incubation or associated stimuli (Slater 1967, Eisner 1969, Hall and Goldsmith 1983). Prolactin levels then increase through laying and peak in the early to mid-incubation period (Breitenbach et al. 1965, Silverin and Goldsmith 1983).

Mead and Morton (1985) proposed that hatching asynchrony is the result of selection on an unrelated trait(s), namely the termination of ovulation and the onset of incubation, with prolactin possibly playing a role in each; in concert with the ovulation of the last ovum, there is a surge in the level of prolactin in the blood. This terminates ovulation and stimulates the initiation of full incubation, which subsequently gives rise to hatching asynchrony (Mead and Morton 1985). Consequently, the advantages derived from hatching asynchrony (e.g. Lack 1954, Hussell 1972, Clark and Wilson 1981, Hahn 1981, Slagsvold and Lifjeld 1989), if any, are merely "epiphenomena."

From their hypothesis, Mead and Morton (1985) predicted that: (1) full incubation attentiveness will begin when the penultimate egg

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TABLE 1. Comparison of mean ($\bar{x} \pm$ SE) incubation attentiveness (seconds per 0.5 h) for female Yellow Warblers tending four- and five-egg clutches. Sample sizes in parentheses. Data combined for 1988–1990. Abbreviations: APEN, day ante-penultimate egg laid; PEN, day penultimate egg laid; and LAST, day last egg laid.

	Clutch size			
Egg	Four-egg	Five-egg	t	P
APEN	296.43 ± 106.32 (16)	518.70 ± 191.10 (10)	1.10	0.32
PEN	971.25 ± 161.25 (20)	813.00 ± 187.65 (9)	0.58	0.56
LAST	1,249.10 ± 128.33 (20)	1,227.36 ± 185.24 (11)	0.09	0.92

tiveness will begin when the penultimate egg is laid (if the hormonal hypothesis is true, we also predict that for Yellow Warblers, *Dendroica petechia*); (2) incubation attentiveness during egg laying, especially on the day the penultimate and last eggs are laid, will be similar in four- and five-egg clutches; (3) hatch spreads will be similar whether clutches contain four or five eggs; and (4) incubation attentiveness will not be affected by experimentally adding eggs during laying. The purpose of our study then was to establish the onset of incubation behavior during laying in the Yellow Warbler and test the above predictions derived from the mechanistic aspect of the "hormonal" hypothesis (Mead and Morton 1985).

The Yellow Warbler is an ideal species for this study because it exhibits hatching asynchrony, generally lays four- or five-egg clutches (Goossen and Sealy 1982) and is a determinate layer (Sealy 1992). This last characteristic is important to Mead and Morton's (1985) hypothesis. These authors argued that hormonal influences should be reflected more accurately in determinate layers that show a characteristic sharp surge in the level of prolactin in the blood and in the onset of incubation behavior, whereas indeterminate layers are characterized by a gradual onset in incubation behavior and more variable clutch sizes (Mead and Morton 1985 and references therein).

METHODS

The study was conducted during the summers of 1988–1990 on a population of Yellow Warblers breeding in the forested dune ridge at Delta Marsh, Manitoba, Canada (50°11'N, 98°19'W; for a description of the study area, see MacKenzie 1982). We searched daily for nests, which we numbered and flagged, and checked daily through clutch completion. Each egg was marked on the blunt end to indicate its position in the laying sequence.

Beginning with the day the second egg was laid, a sample of control and experimental nests (described below) was observed for 0.5 h each day until clutch completion. Observations were made either between 0500 to 0800 or 1745 to 2015 CST. During these observation periods, the number of eggs in the nest was recorded as well as the amount of time females incubated (to the nearest second).

To test experimentally the hormonal hypothesis, we added two eggs to one group of nests on the evening before the second egg was to be laid, or on the morning it was laid. One of the additional eggs was removed on the evening before or the morning on which the fourth egg was laid, and the second was removed the following day. In this manner, experimental nests contained six eggs for only short periods of time, if at all. No observations were made on nests containing six eggs.

The data on incubation attentiveness were grouped for observations made on the days eggs were laid: the ante-penultimate egg (APEN; i.e. second egg in a four-egg clutch, third egg in a five-egg clutch); the penultimate egg (PEN); and the last egg (LAST). Incubation attentiveness between eggs and experimental groups was analyzed using the general linear models (ANOVA with unequal sample sizes) program in SAS (SAS Institute 1985), as well as the Student-Newman-Keuls test for multiple comparisons (Zar 1974). The null hypothesis was rejected when $P < 0.05$.

Finally, to determine whether observed incubation patterns were reflected in subsequent hatching patterns, we recorded hatching spreads in control four- and five-egg clutches between the first- and last-hatched nestlings (FLAST), the ante-penultimate, and last-hatched nestlings (APLAST), and the penultimate and last-hatched nestlings (PLAST). Hatching spreads were determined by visiting each nest at 0500, 1000, 1500, and 1900 during the hatching period.

Because mean ($\bar{x} \pm$ SE) hatching spreads (h) differed significantly among years (see results), we minimized interyear differences between hatching spreads by standardizing them using the method described by Perrins and McCleery (1985). The yearly mean was subtracted from each observation, and the result was divided by the yearly standard deviation. The resulting standardized hatching spreads were compared using two-tailed t-tests.

TABLE 2. Comparison of mean ($\bar{x} \pm$ SE) incubation attentiveness (seconds per 0.5 h) of females tending control or experimental clutches (eggs added during laying). Sample sizes in parentheses. Data combined for 1988–1990. Abbreviations: APEN, day ante-penultimate egg laid; PEN, day penultimate egg laid; and LAST, day last egg laid.

| | Clutch type | | | |
Egg	Control[a]	Experimental	*t*	*P*
APEN	381.92 ± 98.48 (26)	832.30 ± 133.66 (23)	2.75	0.008
PEN	922.13 ± 124.43 (29)	1,226.62 ± 111.99 (24)	1.78	0.08
LAST	1,241.38 ± 103.88 (31)	1,555.00 ± 64.38 (27)	2.47	0.01

[a] The three control means are significantly different from each other.

RESULTS

Incubation attentiveness did not differ between years for females with four- (GLM, $F = 0.86, P = 0.49$) or five-egg (GLM, $F = 0.16, P = 0.95$) clutches. Also, when the data were combined over the three years, females tending four- and five-egg clutches exhibited similar patterns of incubation attentiveness during laying (GLM, $F = 0.65, P = 0.52$; Table 1). Therefore, we combined the data on incubation attentiveness for both clutch sizes.

Mean ($\bar{x} \pm$ SE) incubation attentiveness (s) was significantly affected by the position of the egg in the laying sequence (GLM, $F = 15.14, P = 0.0001$; Table 2). Incubation attentiveness increased significantly through laying (Table 2). Females were more attentive on the day they laid the PEN egg compared with the APEN egg (SNK, $q = 4.74, P < 0.005$), and more attentive on the day they laid the LAST egg compared to the day they laid the APEN egg (SNK, $q = 7.70, P < 0.001$) and the PEN egg (SNK, $q = 2.94, P < 0.05$; Table 2).

Between groups, control females were significantly less attentive on the day the APEN and LAST eggs were laid compared with experimental females (Table 2). Control females also incubated less on the day the PEN egg was laid than did experimental females, a difference that approached significance (Table 2).

In control nests the mean FLAST and APLAST hatching spreads in four- and five-egg nests differed significantly in two of the three years of the study (Table 3). The shorter hatch spreads in both clutch sizes in 1989 were probably due to below-average temperatures that persisted during the laying period (Hébert, unpubl. data). For the three years combined, the standardized FLAST and APLAST hatch spreads were shorter in four- compared with five-egg clutches (Table 3). Likewise, the PLAST hatch spread tended to

TABLE 3. Comparison of mean ($\bar{x} \pm$ SE) hatch spreads (h) for control four- and five-egg clutches. Sample sizes in parentheses.

| | | Clutch size | | | |
Year	Hatch spread[a]	Four-egg	Five-egg	*t*	*P*
1988	FLAST	35.7 ± 3.1 (18)	56.0 ± 2.0 (5)	5.49	0.0001
	APLAST	32.3 ± 3.0 (17)	39.7 ± 1.8 (7)	2.06	0.05
	PLAST	20.7 ± 1.8 (18)	26.1 ± 1.5 (7)	1.74	0.09
1989	FLAST	28.7 ± 2.4 (13)	33.7 ± 2.6 (7)	1.33	0.19
	APLAST	24.8 ± 2.2 (10)	28.2 ± 2.7 (6)	1.06	0.30
	PLAST	18.1 ± 1.3 (13)	18.5 ± 1.5 (8)	0.16	0.86
1990	FLAST	35.5 ± 2.0 (18)	50.4 ± 2.0 (18)	5.22	0.0001
	APLAST	32.0 ± 2.0 (18)	39.1 ± 1.2 (15)	3.02	0.005
	PLAST	21.5 ± 0.7 (18)	22.6 ± 0.7 (18)	1.06	0.29
Combined standardized[b]	FLAST	−0.41 ± 0.1 (49)	0.67 ± 0.1 (30)	5.57	0.0001
	APLAST	−0.28 ± 0.1 (45)	0.45 ± 0.1 (28)	3.31	0.001
	PLAST	−0.14 ± 0.1 (49)	0.22 ± 0.1 (33)	1.69	0.09

[a] FLAST, hatch spread between first- and last-hatched nestling; APLAST, hatch spread between ante-penultimate and last-hatched nestling; PLAST, hatch spread between penultimate and last-hatched nestling.

[b] See methods for explanation.

TABLE 4. Comparison of mean ($\bar{x} \pm$ SE) standardized hatch spreads between control clutches and those to which eggs were added during laying. Sample sizes in parentheses. Data for 1988 and 1989 combined.

Clutch size	Hatch spread[a]	Clutch type		t	P
		Control	Experimental		
4	FLAST	-0.02 ± 0.2 (31)	0.13 ± 0.3 (5)	0.32	0.37
	APLAST	0.005 ± 0.2 (27)	-0.04 ± 0.5 (3)	0.07	0.47
	PLAST	-0.03 ± 0.2 (31)	0.28 ± 0.5 (4)	0.59	0.28
5	FLAST	-0.87 ± 1.3 (12)	1.75 ± 1.4 (6)	1.25	0.11
	APLAST	-0.12 ± 0.2 (13)	0.33 ± 0.6 (5)	0.87	0.20
	PLAST	-0.10 ± 0.3 (15)	0.26 ± 0.3 (6)	0.75	0.27

[a] For definition of terms, see Table 3.

be shorter in four-egg as opposed to five-egg clutches, and this difference approached significance (Table 3).

Since females tending control clutches were significantly less attentive during egg laying than females tending nests to which eggs were added experimentally, the a priori prediction was made that hatching spreads would also be shorter in control nests. In general, hatch spreads were shorter in control nests (Table 4). However, only the difference in the FLAST hatch spread in control and experimental five-egg clutches approached significance (Table 4).

DISCUSSION

The prediction of the hormonal hypothesis (Mead and Morton 1985) that full incubation behavior begins with the laying of the penultimate egg is not supported by our results. Incubation attentiveness of female Yellow Warblers increased steadily through laying. Contrary to the hormonal hypothesis, full incubation did not begin with the laying of the penultimate egg in either four- or five-egg clutches, but rather was delayed until the last egg was laid, and possibly later. Females with four- and five-egg clutches spent only 54% and 45% of their time, respectively, incubating the penultimate egg. This increased to 67% and 68%, respectively, for the last egg. Furthermore, full incubation may have been delayed until after clutch completion. In a small sample ($n = 8$) of observations one to three days after clutch completion, we observed that female Yellow Warblers spent about 78% of their time incubating. Similarly, Sutherland (1987) observed that incubation attentiveness by female Yellow Warblers, two days after clutch completion, averaged about 80%. This agrees with the evidence that the blood level of the hormone that influences incubation behavior increases steadily

during the egg-laying/incubation period (Silverin and Goldsmith 1983, see also review in Drent 1975). Full daytime incubation also is delayed until the laying of the last egg by Common Grackle (Quiscalis quiscula) females producing three- or four-egg clutches, but females producing five- or six-egg clutches initiate incubation prior to clutch completion (Howe 1978). Similar delays in the onset of full daytime incubation have been observed in the Mountain White-crowned Sparrow (Zonotrichia leucophrys oriantha; Zerba and Morton 1983) and the Great Tit (Parus major; Haftorn 1981).

That Yellow Warbler females producing four- and five-egg clutches exhibited similar patterns of incubation attentiveness, especially on the day the PEN and LAST eggs were laid, agrees with the hormonal hypothesis. From Mead and Morton's (1985) hypothesis, we predicted that incubation attentiveness should be similar between females producing clutches of different sizes, since the hormonal influences associated with the ovulation of the last egg should be similar regardless of clutch size. However, the power (see Cohen 1988, Forbes 1990) of the t-tests accepting the null hypothesis (see Table 1) was weak (ca. 10–20%). Thus, it is possible that incubation attentiveness, especially on the day the APEN egg was laid (see Table 1), differed between females producing four- and five-egg clutches, but our sample size is too small to detect this difference. Nevertheless, if incubation attentiveness during egg laying is similar for females producing clutches of different sizes, then a corollary prediction would be that hatching spreads would also be similar. Our data do not support the prediction, since we observed significant differences between clutch sizes in two of three measures of standardized hatching spreads (FLAST and APLAST). The significant difference in the FLAST hatch spread between four- and five-egg clutches could, at

least partially, be explained by the fact that there is one more egg in a five-egg clutch, and that there is some incubation before the penultimate egg is laid. There should not be, however, any differences in the APLAST and PLAST hatch spreads. Nevertheless, the APLAST hatch spreads recorded in the present study differed significantly between four- and five-egg clutches. The difference in the PLAST hatch spread approached significance ($P = 0.09$). These results are in contrast to the attentiveness patterns observed during laying, which suggests that hatch spreads may be affected by variations in attentiveness patterns during early egg laying.

Several studies of asynchronous hatching in passerines also have reported significant differences in hatch spreads among different clutch sizes (e.g. Smith 1988, Briskie and Sealy 1989, Stouffer and Power 1990). Smith (1988) found that asynchronous hatching was greater in Dark-eyed Junco (*Junco hyemalis*) clutches of five eggs compared to four-egg clutches, and Stouffer and Power (1990) observed a similar trend in four- and five-egg European Starling (*Sturnus vulgaris*) clutches. Similar results have been observed in other species (e.g. Least Flycatchers, *Empidonax minimus*, Briskie and Sealy 1989; House Martins, *Delichon urbica*, Bryant 1978; Common Grackles, Howe 1978). Again, the results of the present study, and evidence from other studies, clearly do not support the hormonal hypothesis because hatch spreads are not similar in different clutch sizes.

A key element in Mead and Morton's (1985) argument is the fact that Mountain White-crowned Sparrows delay nighttime incubation until the penultimate egg has been laid, and this delay is reflected in the hatching spreads. However, the proportion of Yellow Warbler females sitting in nests at night does not change from the night after the first egg is laid through clutch completion, regardless of whether the female eventually produces four or five eggs (R. M. R. Barclay et al., unpubl. manuscript). Again, this suggests that incubation behavior of Yellow Warblers is not regulated by hormonal fluxes associated with the laying of the penultimate egg, since females begin nighttime roosting well before they lay the penultimate egg. Barclay et al. (unpubl. manuscript) observed that, although a certain proportion of female Least Flycatchers roosted overnight in their nests prior to laying the last egg (varying from 29 to 40% for the first three eggs laid), the majority of females delayed nighttime atten-

tiveness until the last egg was laid (83%, $n = 6$). Also, of six female Dusky Flycatchers (*E. oberholseri*) observed by Morton and Pereyra (1985), three initiated nighttime sitting on the day the ante-penultimate egg was laid, and three began on the day the penultimate egg was laid. In fact, in most species observed, females exhibit some nighttime and/or daytime attentiveness from the day the first egg is laid (e.g. Weeden 1966, Haftorn 1979, 1981, Zerba and Mortin 1983, Morton and Pereyra 1985, Briskie and Sealy 1989), including Yellow Warblers (Barcaly et al., unpubl. manuscript). This, in conjunction with hatch spreads that vary among clutch sizes, suggests that daytime and nighttime incubation may be controlled separately (M. Morton, pers. comm.), and that hatch spreads are not affected by hormonal surges coincidental with the laying of the penultimate egg, or by nighttime attentiveness patterns, but rather result from subtle changes in daytime incubation attentiveness before the penultimate egg is laid.

If initiation of incubation behavior is rigidly controlled by hormonal fluxes associated with the ovulation of the last ova, then it would be predicted that adding eggs to a clutch prior to the laying of the penultimate egg would not affect incubation attentiveness. Our results show that females can be induced to begin incubating prior to laying the penultimate egg. That is, females tending control clutches were significantly less attentive than females with clutches to which eggs were added early during laying. Similar results were obtained by Beukeboom et al. (1988) in the Eurasian Kestrel (*Falco tinnunculus*).

From the above, it can also be predicted that hatch spreads will be shorter in control nests compared to nests in which eggs were added during egg laying. This prediction, however, was not supported by the results of our study, since only the difference in FLAST hatch spreads between control and experimental five-egg clutches approached significance ($P = 0.11$). Nevertheless, the trends are in the direction predicted in that hatch spreads generally were longer in experimental nests. Hence, the overall increase in female attentiveness and hatch spreads indicate that rigid control of incubation behavior, by endogenously regulated hormonal fluxes alone, does not appear likely.

Finally, if hatching patterns were controlled rigidly by hormonal activities associated with the ovulation of the last egg, we would expect little variation in hatching spreads among

clutches, clutch sizes, seasons, and years. However, there is evidence that hatch spreads vary among clutches of different sizes (e.g. Mead and Morton 1985, Briskie and Sealy 1989, this study), seasonally (e.g. Mead and Morton 1985, Slagsvold 1986), and yearly (this study). This suggests that hormonal influences on incubation behavior do not preclude variation in hatch spreads. Some of this variation in hatch spreads is likely to be genetic and, therefore, influenced by natural selection (Magrath 1990). Hence, contrary to the hormonal hypothesis, advantages accrued through hatching asynchrony may be adaptive (e.g. Lack 1954, Hahn 1981, Slagsvold and Lifjeld 1989).

However, our experimental results (see also Slater 1967, Beukeboom et al. 1988) also concur with previous studies showing that tactile stimuli (Hall and Goldsmith 1983) and/or temperature stimuli (White and Kinney 1974) from the eggs via the brood patch play a role in controlling incubation attentiveness during laying. Furthermore, the effect of these stimuli can also be moderated by other stimuli such as hunger, or stimuli from the environment (White and Kinney 1974, see also Slater 1967). Thus, any hypothesis regarding the causal mechanisms producing hatching asynchrony should include the effects of other stimuli, as well as hormonal influences.

In conclusion, the hormonal hypothesis as originally stated does not adequately explain hatching asynchrony in species where only females incubate. Incubation attentiveness patterns of laying Yellow Warblers suggest that full incubation does not begin when the penultimate egg is laid, as predicted by the hormonal hypothesis. That is, hatching asynchrony apparently does not require full daytime incubation attentiveness during laying, or an abrupt onset with the penultimate egg. Hatch spreads in Yellow Warblers and other species surveyed, in contrast to that predicted by the hormonal hypothesis, differed significantly among clutch sizes, and these differences may be related to small differences in incubation attentiveness during laying. In addition, eggs added experimentally during laying increased incubation attentiveness, which suggests that incubation behavior, although under hormonal control, is not rigid and is not associated only with hormonal fluxes associated with the ovulation of the last ova.

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