

THE FUNCTION OF EARLY ONSET OF NOCTURNAL INCUBATION IN RED-WINGED BLACKBIRDS

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ABSTRACT.—We examined variation in the onset of nocturnal incubation by female Red-winged Blackbirds (*Agelaius phoeniceus*). Many females began nocturnal incubation after laying the prepenultimate egg, which resulted in asynchronous hatching. This pattern of incubation is consistent with a model that predicts hatching asynchrony when the ratio of nest predation in the egg stage to predation in the nestling stage is near unity. Using 13 years of nest data, however, we found no significant relationship between the natural degree of hatching asynchrony and fledging success, and a significant negative relationship between hatching asynchrony and nestling quality. Therefore, we considered three hypotheses to explain the early onset of nocturnal incubation in this species: (1) increased egg viability, (2) protection of clutches from predators, and (3) protection of clutches from brood parasitism by Brown-headed Cowbirds (*Molothrus ater*). We found no evidence that early onset of nocturnal incubation increased egg viability. Incubation was not related to ambient temperature or precipitation, and early onset of incubation was not associated with increased hatching success. Nocturnal incubation was similar at depredated and nondepredated nests, which does not support the hypothesis that nest predation selects for early onset of incubation. Onset of nocturnal incubation occurred significantly later at nests parasitized by cowbirds than at unparasitized nests, however, in one of two years. These data suggest that protection against cowbird parasitism favors early onset of nocturnal incubation in Red-winged Blackbirds. Received 11 November 1997, accepted 9 September 1998.

EGGS WITHIN A CLUTCH may hatch synchronously on the same day or asynchronously over a period of days (Clark and Wilson 1981). Lack (1947, 1968) proposed the brood-reduction hypothesis, which posits that hatching asynchrony is an adaptive response whereby brood size is adjusted to match food availability. Lack's hypothesis has been supported by some studies (Husby 1986, Lessells and Avery 1989, Magrath 1989, Hébert 1993, Wiebe and Bortolotti 1995) but not by others (Skagen 1988, Bollinger et al. 1990, Amundsen and Slagsvold 1991, Seddon and van Heezik 1991, Harper et al. 1992). Clark and Wilson (1981) presented the hypothesis that hatching asynchrony increases the probability that at least one nestling survives. This nest-failure model has been influential but has received little empirical support (Amundsen and Stokland 1988, Briskie and Sealy 1989, Hébert and Sealy 1993).

Since Clark and Wilson's (1981) model, many explanations for hatching asynchrony have been proposed, but few have found widespread support (see Magrath 1990, Slagsvold et al.

1995, Stoleson and Beissinger 1995, Stenning 1996). Most studies, however, have found that hatching asynchrony has a neutral or negative effect on fledging success and nestling quality, especially when environmental conditions are favorable (Nilsson 1995, Stoleson and Beissinger 1995). This result has prompted researchers to consider that hatching asynchrony is an epiphenomenon of hormonal changes associated with egg laying (Mead and Morton 1985), or that it may increase the survival of eggs or adults but not benefit nestlings (Beissinger and Waltman 1991, Martin 1992, Hörak 1995, Beissinger et al. 1998).

Asynchronous hatching is assumed to result when eggs are incubated before clutch completion, although this assumption is infrequently tested (Clark and Wilson 1981, Lessells and Avery 1989, Bortolotti and Wiebe 1993, Wiebe et al. 1998). Diurnal nest attentiveness usually begins early in the egg-laying period (Skutch 1962; Weeden 1966; Haftorn 1981, Zerba and Morton 1983a, b; Lessells and Avery 1989), but nocturnal incubation often is delayed until after the ultimate or penultimate egg is laid, at which time full incubation begins (Holcomb

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1974, Nolan 1978, Mead and Morton 1985, Morton and Pereya 1985, Meijer 1990). The little available information on nocturnal incubation suggests that its onset is highly variable, both within and between species (Haftorn 1981, Brackbill 1985, Neudorf and Sealy 1994; but see Beissinger and Waltman 1991).

Here, we examine the onset of nocturnal incubation and the resulting hatching asynchrony in Red-winged Blackbirds (*Agelaius phoeniceus*). This species is ideal for such a study because only females incubate, individual differences in incubation and hatching asynchrony exist, and many aspects of this species' breeding biology are well known. Specifically, we examined whether early onset of incubation by female Red-winged Blackbirds (hereafter "redwings") causes asynchronous hatching, and if asynchronous hatching results in greater fledging success and/or increased nestling quality. We used nocturnal incubation as an indicator of the onset of incubation. We also tested three hypotheses for the early onset of nocturnal incubation. The egg-viability hypothesis (Arnold et al. 1987, Veiga 1992, Veiga and Viñuela 1993) posits that females begin incubation earlier in the clutch at low ambient temperatures or during periods of high precipitation. From this hypothesis, we also predicted that early onset of nocturnal incubation would result in higher hatching success. The second hypothesis was the predation hypothesis (Dunlop 1910, Bollinger et al. 1990), which predicts that early onset of nocturnal incubation is associated with decreased predation during the egg-laying period. Third, we tested the brood-parasitism hypothesis (Ricklefs 1969), which states that early onset of nocturnal incubation is associated with reduced rates of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*).

METHODS

Study area.—We studied Red-winged Blackbirds from April to July in 1996 and 1997 at two contiguous grass and sedge meadows in Rock County, Wisconsin (42°32'N, 89°08'W). The redwings at one of these sites, Newark Road Prairie (NRP), have been studied extensively by Yasukawa and his colleagues (e.g. Yasukawa 1989; Yasukawa et al. 1990, 1992). A detailed description of the site can be found in those references. The second site, Diehls Prairie (DP), is a 12-ha oldfield/prairie and is similar in many respects to NRP. NRP and DP support 25 to 30 and 30 to 35 territorial male redwings each year, respectively, and

males in these areas usually have two to three females nesting on their territories (Searcy and Yasukawa 1995). Redwings in southern Wisconsin breed from early May until early July and are parasitized by Brown-headed Cowbirds throughout the breeding season. Cowbirds parasitize 2 to 23% of redwing nests on NRP and 15 to 33% on DP (Yasukawa et al. 1990, Clotfelter 1998a). We removed cowbird eggs from all redwing nests on NRP 2 to 24 h after laying (for purposes unrelated to the current study), but eggs were not removed from nests at DP.

Effects of natural hatching asynchrony.—To assess the relationship between natural variation in hatching asynchrony and reproductive success, we used NRP nest-record data from 1984 to 1996. Hatching asynchrony was measured as the number of days between first- and last-hatched eggs. We checked all nests daily; if all eggs in a clutch hatched between consecutive visits, we recorded the hatching asynchrony as 0 days. Simultaneous multiple regressions were used to determine the relative importance of hatching asynchrony, nest-initiation date, nest status (the chronological sequence of nests within a male's territory), clutch size (range 2 to 5), and study year on three dependent variables: fledging success (number of fledglings per nest, range 0 to 4), body mass (measured 7 to 8 days posthatching), and tarsus length (7 to 8 days posthatching). Redwing nestlings typically leave the nest after 12 days, but we considered birds to have fledged if they survived at least 10 days after hatching. Nests producing no fledglings were excluded from analyses of body mass and tarsus length.

We used data from NRP nest records for 1989 to 1996 (the years with the most complete data) to calculate daily nest-predation rates during the egg and nestling stages. Daily predation rates were calculated as the number of depredated nests divided by the number of days of observation (Mayfield 1961). Calculations were performed separately for the egg stage (egg laying + incubation) and nestling stage, and from these we calculated daily survival rates (P_1 and P_2). We used P_1 and P_2 to calculate the optimal day for initiating incubation (m) according to the model of Clark and Wilson (1981: fig. 2), where a plot of $(1 - P_2)/(1 - P_1)$ versus P_1 gives the parameter spaces for various values of m . We used Clark and Wilson's (1981) model instead of Hussell's (1985) revised nest-failure model because we were unable to accurately estimate the parameters P_0 and P_3 , which are essential to the latter model.

Onset of nocturnal incubation.—We collected data on nocturnal incubation from 12 to 22 May 1996 and 13 May to 11 June 1997. Two methods were employed to determine when individual females began nocturnal incubation. In 1996, we inspected nests between 0230 and 0330 CST. We used these times because morning arrival of redwings roosting away from the breeding grounds begins approximately 30

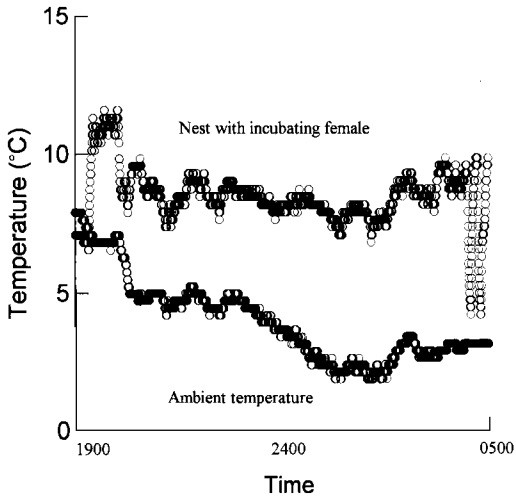


FIG. 1. Temperature profile from an active Red-winged Blackbird nest compared with the profile from an ambient temperature probe. Temperature was recorded every 12 s between approximately 1900 and 0500 CST. The active nest contained three Red-winged Blackbird eggs. On the basis of these profiles, we determined that the female incubated the clutch overnight.

min before sunrise (Neudorf and Sealy 1994). Sunrise occurred between 0429 and 0439 during the 1996 study period. Therefore, we assumed that females observed on their nests before 0330 had been there overnight (Nolan 1978, Neudorf and Sealy 1994). To minimize disturbance, we used night-vision goggles (NVAC 800 Night Vision System) to detect female redwings on their nests. If no female was seen, an egg from the clutch was touched against the investigator's lips to determine if it had been incubated. If the egg was warm, we assumed the female had incubated overnight. We monitored nests for four consecutive mornings following the laying of the first egg.

In 1997, we monitored nocturnal incubation by inserting temperature probes into nest linings. Probes were connected to data loggers 1 to 2 m from nests and recorded temperature ($\pm 0.5^\circ\text{C}$) every 12 s. Data loggers recorded continuously for 20 to 26 h and were removed from nests, downloaded in the field, and replaced at nests between 0800 and 0900. We compared temperature profiles from active nests with profiles of ambient temperature to determine when females were present on the nest (Fig. 1). We placed the ambient temperature probe in an abandoned redwing nest to approximate thermal conditions of an unattended nest. All probes were placed in the southern wall of nests to standardize among nests and to reduce the effects of direct sunlight. We confirmed the accuracy of this method by comparing

temperature profiles with videotapes from a subsample of nests ($n = 6$). Videotapes showed that nest temperature usually reached an asymptote within 5 min after the arrival or departure of a female redwing.

Hatching asynchrony and success, nest predation, and brood parasitism.—For all nests for which we obtained data on nocturnal incubation, we recorded hatching success (the proportion of total eggs laid that hatched) and the degree of hatching asynchrony (number of days between the first-hatched and last-hatched eggs; range zero to three). We also noted whether brood parasitism by Brown-headed Cowbirds or nest predation occurred during the egg-laying period.

Temperature and precipitation.—Temperature and precipitation data were obtained from the Beloit College NOAA weather station, approximately 13 km from the study sites. For each day in the 1996 and 1997 study periods, minimum temperature, maximum temperature, and total precipitation during the 24-h period are reported.

Female age class.—Female redwings for which we had incubation information were classified as ASY (after second year) or SY (second year) on the basis of plumage coloration (Johnsen et al. 1996). Classification of each female was made by a naive observer. During the first year of study we used five color-banded females of known breeding experience as an independent test of the accuracy of this classification method. The naive observer correctly classified all five females. Females that could not be classified unambiguously were excluded from the analysis.

Statistical analyses.—To avoid the potentially confounding effect of clutch size, we scored the onset of nocturnal incubation as the egg after which nocturnal incubation began divided by the total clutch size. Therefore, a female who incubated the night after the first egg of a 4-egg clutch received a score of 0.25. These proportions were arcsine-transformed and are presented in gradient units (Sokal and Rohlf 1981). Simultaneous multiple linear regression, logistic regression, *t*-tests, and Kruskal-Wallis tests were performed using SYSTAT (Wilkinson 1996). All tests are two-tailed, and all means are presented ± 1 SE.

RESULTS

Effect of natural hatching asynchrony.—Natural variation in hatching asynchrony at NRP from 1984 to 1996 is shown in Table 1. These nest records also show that hatching asynchrony was unrelated to fledging success but was negatively related to nestling quality as measured by body mass and tarsus length at 7 to 8 days post-hatching (Table 2). Nest-initiation date and study year had significant negative effects on

TABLE 1. Yearly variation in hatching asynchrony (days between first- and last-hatched eggs) in Red-winged Blackbird clutches at Newark Road Prairie, 1984 to 1996. Values are the number of clutches that hatched over a given period of days.

	Hatching asynchrony (days)			
	0	1	2	3
1984	2	19	2	0
1985	3	22	8	0
1986	9	18	2	0
1987	8	16	7	0
1988	0	32	10	0
1989	5	22	2	0
1990	9	28	8	0
1991	2	24	10	1
1992	11	51	7	2
1993	6	31	7	0
1994	4	17	8	0
1995	9	22	3	0
1996	5	9	2	2
Total	73 (15.7%)	311 (66.9%)	76 (16.3%)	5 (1.1%)

fledging success and nestling quality. First nests in a male's territory produced significantly more fledglings than later nests, but nestling quality was unaffected by this estimate of nest status. Neither fledging success nor nestling quality was affected by clutch size.

Onset of nocturnal incubation.—We observed nocturnal incubation for part or all of egg laying for 40 and 45 female redwings in 1996 and 1997, respectively. Of these, we obtained accurate information on the onset of nocturnal in-

cubation for 31 and 38 females, many of which began nocturnal incubation following the prepenultimate egg (Table 3). Females that began nocturnal incubation after the ultimate egg had significantly smaller clutches than females incubating after the prepenultimate or penultimate eggs in one year of the study (Table 3). None of the 40 females observed in 1996 abandoned their nests. Seven females abandoned their nests in 1997, probably in response to the temperature probes. There was no relationship

TABLE 2. Variables affecting fledging success (young per brood), mean body mass, and mean tarsus length in Red-winged Blackbird nestlings at Newark Road Prairie, 1984 to 1996. Shown are unstandardized linear regression coefficients (\pm SE), partial-*t* values, and *P*-values. Sample sizes are number of broods.

Variable	Fledging success (<i>n</i> = 465)	Body mass (<i>n</i> = 228)	Tarsus length (<i>n</i> = 227)
Constant	4.70 \pm 0.86 <i>t</i> = 5.44 <i>P</i> < 0.001	47.73 \pm 3.81 <i>t</i> = 12.52 <i>P</i> < 0.001	34.73 \pm 1.67 <i>t</i> = 20.89 <i>P</i> < 0.001
Hatching asynchrony	0.11 \pm 0.11 <i>t</i> = 0.97 <i>P</i> = 0.333	-1.08 \pm 0.48 <i>t</i> = -2.27 <i>P</i> = 0.025	-0.51 \pm 0.21 <i>t</i> = -2.44 <i>P</i> = 0.016
Julian date	-0.02 \pm 0.004 <i>t</i> = -4.41 <i>P</i> < 0.001	-0.074 \pm 0.02 <i>t</i> = -3.59 <i>P</i> < 0.001	-0.02 \pm 0.01 <i>t</i> = -2.18 <i>P</i> = 0.03
Study year	-0.07 \pm 0.02 <i>t</i> = -3.31 <i>P</i> = 0.001	-0.31 \pm 0.08 <i>t</i> = -4.04 <i>P</i> < 0.001	-0.09 \pm 0.03 <i>t</i> = -2.78 <i>P</i> = 0.006
Nest status	-0.29 \pm 0.11 <i>t</i> = -2.55 <i>P</i> = 0.011	-0.92 \pm 0.52 <i>t</i> = -1.75 <i>P</i> = 0.081	-0.20 \pm 0.23 <i>t</i> = -0.89 <i>P</i> = 0.374
Clutch size	0.10 \pm 0.12 <i>t</i> = 0.88 <i>P</i> = 0.381	-0.71 \pm 0.51 <i>t</i> = -1.39 <i>P</i> = 0.166	-0.15 \pm 0.22 <i>t</i> = -0.68 <i>P</i> = 0.498

TABLE 3. Summary of nocturnal incubation data, 1996 and 1997. Prepenultimate, penultimate, and ultimate refer to the egg after which nocturnal incubation began. Clutch size is $\bar{x} \pm SE$ for each group; *P*-values are from Kruskal-Wallis ANOVA for differences among clutch sizes within years.

	Onset of incubation			<i>P</i> -value
	Prepenultimate	Penultimate	Ultimate	
1996				
No. of nests	14	5	12	<i>P</i> = 0.66
Clutch size	3.79 ± 0.16	3.60 ± 0.25	3.33 ± 0.31	
1997				
No. of nests	12	16	10	<i>P</i> = 0.001
Clutch size	3.92 ± 0.08	3.38 ± 0.13	2.90 ± 0.23	

between the 1996 nocturnal nest inspections and nest predation: daily predation rate during this period (0.051 nests depredated per nest day) was comparable to the daily nest-predation rate calculated from NRP nest records (see below). The temperature probe data support our assumption that nest checks conducted between 0230 and 0330 in 1996 were accurate indications of nocturnal incubation (Fig. 1). These data also suggest that female redwings were incubating their clutches at night rather than roosting near them (Haftorn 1981).

Hatching asynchrony.—We determined the degree of hatching asynchrony for clutches of 21 and 17 females in the 1996 and 1997 focal groups, respectively. Nine clutches hatched synchronously (zero days between the first- and last-hatched eggs) and 12 hatched asynchronously (over one day) in 1996. In 1997, 7 clutches hatched synchronously and 10 hatched asynchronously. Early incubation resulted in greater asynchrony. Females whose clutches hatched asynchronously (mean arcsine-transformed proportions, 1996, 0.84 ± 0.08; 1997, 0.81 ± 0.09) initiated incubation one egg earlier, on average, than females that produced synchronous clutches (1996, 1.37 ± 0.10; 1997, 1.25 ± 0.12). This difference was significant in both years of the study (1996, $t = -4.09$, $df = 16$, $P = 0.008$; 1997, $t = -2.96$, $df = 13$, $P = 0.011$).

Hatching success.—Hatching success was known for 26 and 22 nests in 1996 and 1997. Hatching success generally was high regardless of the onset of incubation (1996, 0.88 ± 0.04 of all eggs hatched; 1997, 0.87 ± 0.04 of all eggs hatched). In neither year was hatching success significantly correlated with the timing of onset of nocturnal incubation (1996, $r = 0.15$, $P = 0.46$; 1997, $r = 0.08$, $P = 0.71$).

Temperature and precipitation.—We used logistic regression to determine which factors significantly affected incubation in female Red-winged Blackbirds. We considered the following variables: maximum daily temperature (range 11 to 31.1°C), minimum daily temperature (range 0.6 to 21.7°C), daily precipitation (range 0 to 37.6 mm), Julian date, and night in the laying sequence (one to four). We also included a dummy variable for year because of the different methods used (see above), as well as all interaction terms. The best model was the one that included only the night in the laying sequence ($r^2 = 0.15$, $\chi^2 = 44.7$, $df = 3$, $P < 0.001$). None of the other variables, including minimum temperature, maximum temperature and precipitation, had a significant effect on the probability that a given female incubated on a given night.

Predation.—Based on data collected at NRP from 1989 to 1996, daily rates of predation on Red-winged Blackbird nests were 0.047 during the egg stage and 0.053 during the nestling stage. We used these predation rates to calculate a nest-failure ratio ($1 - P_2 / 1 - P_1$) of 1.13. From this ratio, we determined the optimal onset of incubation (m) as taking place after the first egg (Clark and Wilson 1981: fig. 2).

Of the nests in the focal groups, 5 and 15 suffered predation in 1996 and 1997, respectively, whereas 26 and 22 nests were not depredated. We found no difference in the onset of nocturnal incubation by females of depredated and non-depredated nests (mean arcsine-transformed proportions; 1996, depredated = 1.08 ± 0.21, non-depredated = 1.09 ± 0.08; $t = -0.05$, $df = 5$, $P = 0.96$; 1997, depredated = 1.12 ± 0.08, non-depredated = 0.99 ± 0.08; $t = 1.15$, $df = 33$, $P = 0.26$). There also were no differences in clutch size between depredated (1996, 3.80 ±

0.20 eggs; 1997, 3.40 ± 0.16 eggs) and non-depredated (1996, 3.54 ± 0.17 eggs; 1997, 3.45 ± 0.14 eggs) clutches in either year.

Brood parasitism.—Brown-headed Cowbirds parasitized seven and eight redwing nests in the 1996 and 1997 focal groups, respectively. Females that were parasitized began nocturnal incubation later than unparasitized females in one year of the study but not in the other (mean arcsine-transformed proportions; 1996, parasitized = 1.46 ± 0.11 , unparasitized = 0.98 ± 0.08 ; $t = 3.52$, $df = 12$, $P = 0.004$; 1997, parasitized = 1.15 ± 0.13 , unparasitized = 1.03 ± 0.06 ; $t = 0.81$, $df = 11$, $P = 0.43$). We found no evidence that parasitized and unparasitized nests differed in clutch size, but a direct comparison was difficult because cowbirds remove eggs from most, but not all, parasitized redwing nests (see Weatherhead 1989, Røskaft et al. 1990, Clotfelter 1998a).

Female age class.—Of the 31 and 38 females in 1996 and 1997, we were able to classify 27 and 13 of them as ASY or SY birds. We monitored incubation of 12 ASY and 15 SY females in 1996 and 10 ASY and 3 SY females in 1997. We found no consistently significant relationship between female age class and incubation pattern. In 1996, however, ASY females tended to begin nocturnal incubation earlier in the clutch than did SY females (mean arcsine-transformed proportions, 1996, ASY = 0.92 ± 0.10 , SY = 1.18 ± 0.12 ; $t = -1.75$, $df = 25$, $P = 0.09$; 1997, ASY = 0.94 ± 0.11 , SY = 0.99 ± 0.04 ; $t = -0.39$, $df = 10$, $P = 0.70$).

DISCUSSION

The onset of nocturnal incubation by female Red-winged Blackbirds was highly variable, as reported also by Neudorf and Sealy (1994). Holcomb (1974) stated that redwings began incubation following the penultimate or ultimate egg, but we found that 30 to 45% of females initiated nocturnal incubation after the prepenultimate egg. Clutches in which females began nocturnal incubation after the prepenultimate egg hatched more asynchronously than clutches in which incubation began after the penultimate or ultimate egg. In one year of our study, the onset of nocturnal incubation was related to clutch size, as has been reported in previous studies (Meijer 1990, Beissinger and Waltman 1991, Hébert and Sealy 1992). By di-

viding the number of the egg after which nocturnal incubation began by the total number of eggs, we avoided some of the problems associated with variation in clutch size. The use of such a measure may be problematic if hatching success, predation, or parasitism are related to clutch size. We found no evidence for such relationships, however. The degree of hatching asynchrony we observed was consistent with that in other populations of redwings (Holcomb 1974, Strehl 1978, L. S. Forbes pers. comm.).

Our estimated nest-failure ratio was lower than that found in other studies of redwings (see Ricklefs 1969). This difference may have resulted because the other studies did not use Mayfield's (1961) method to estimate daily nest survival rates and thus may have overestimated nest survival during the egg stage. The daily predation rates we observed were similar to those found by Robertson (1972) for upland-nesting redwings in Connecticut. The low nest-failure ratio and the early onset of nocturnal incubation we observed are consistent with Clark and Wilson's (1981) nest-failure model. Relatively low predation rates during the nestling stage favor increased hatching asynchrony, and consequently early incubation, to guarantee that at least some offspring survive. In other studies (e.g. Hébert and Sealy 1993), however, daily nest-predation rates have not predicted the onset of incubation accurately. Our results are also consistent with a recent stochastic model proposed by Stoleson and Beissinger (1995), which predicts a significant increase in the expected number of fledglings produced when incubation begins after the second egg (in five-egg clutch) rather than after the first egg. In both years of our study, more than 30% of females that produced four-egg clutches began incubation after the second egg.

We found no evidence, however, that hatching asynchrony caused by early onset of incubation increased fledgling production. Thirteen years of nesting data showed that hatching asynchrony was unrelated to fledging success and significantly negatively related to nestling quality (body mass and tarsus length). The observed reduction in nestling quality possibly was due to asymmetric competition among nestlings (Bancroft 1985, Hillstrom and Olsson 1994, Wiebe and Bortolotti 1995). However, several studies have shown that asynchrony pro-

motes increased nestling quality (Magrath 1989, Slagsvold et al. 1995, Amundsen and Slagsvold 1996). Our study differed from many previous studies of hatching asynchrony in that we compared naturally asynchronous and synchronous broods and performed no experimental manipulations. Although there are limitations to correlational studies, our results are consistent with experimental studies that have found no benefit of hatching asynchrony in either fledging success or nestling quality (see Nilsson 1995, Stoleson and Beissinger 1995). Therefore, we considered three alternative explanations for the early onset of nocturnal incubation in Red-winged Blackbirds.

If early onset of nocturnal incubation functions to increase egg viability, then females should be more likely to incubate clutches on cold and/or rainy nights. We found no evidence to support this prediction. In our logistic regression model, the only variable that significantly influenced the probability of incubation was the night in the laying sequence. Temperature and precipitation were not related to the probability that a female incubated. Most studies of diurnal incubation report negative relationships between nest attentiveness and ambient temperature (Zerba and Morton 1983a, Cartar and Montgomerie 1985, Smith and Montgomerie 1992, Norment 1995). Comparatively few studies have examined the relationship between temperature and nocturnal incubation (Zerba and Morton 1983b, Morton and Pereya 1985).

Another prediction of the egg-viability hypothesis is that the early onset of nocturnal incubation should increase hatching success. Arnold et al. (1987) found such an increase in hatching success for prairie-nesting ducks, and Veiga (1992) and Veiga and Viñuela (1993) found that early onset of incubation in House Sparrows (*Passer domesticus*) promoted increased hatching success of early laid eggs. We did not mark individual eggs, so we were unable to determine order-specific hatching success. Overall hatching success, however, did not differ among females incubating at different stages. Therefore, we cannot invoke increased hatching success as an explanation for early onset of nocturnal incubation in Red-winged Blackbirds.

The early onset of nocturnal incubation may increase nesting success by protecting eggs

from predators (Dunlop 1910, Amundsen and Stokland 1988, Bollinger et al. 1990). Although many passerines react aggressively toward real and artificial predators during incubation, the effectiveness of such aggression is rarely tested empirically (see Martin 1992). In our study, clutches of female redwings that began incubating early in the egg-laying period were depredated at rates that were similar to those of females that began incubating later. This suggests that early onset of nocturnal incubation does not function primarily as an antipredator defense. This is a reasonable conclusion given that female redwings are unlikely to deter mink (*Mustela vison*) and raccoons (*Procyon lotor*), which are the most common nocturnal predators in our study area (Knight et al. 1985, Yasukawa 1989). Because we focused on nocturnal incubation, we cannot address the possibility that diurnal incubation may be related to predation by species such as American Crows (*Corvus brachyrhynchos*), Sedge Wrens (*Cistothorus platensis*), and bullsnakes (*Pituophis melanoleucus*). In addition, predation is sufficiently variable that a two-year study of modest sample size may be insufficient to reject it as a factor that influences incubation.

Early onset of nocturnal incubation in redwings may also function as a defense against brood parasitism by Brown-headed Cowbirds (Ricklefs 1969). Cowbird parasitism usually occurs before dawn, and a previous study suggested that only birds incubating overnight are present early enough in the morning to defend their nests (Scott 1991, Neudorf and Sealy 1994). Our results were consistent with this hypothesis. Females whose nests were subsequently parasitized began nocturnal incubation later than did females whose nests escaped parasitism. This finding suggests that female redwings can deter intruding cowbirds, which is supported by observations of female redwings in the same population attacking taxidermic mounts of female cowbirds (Clotfelter 1998b). Neudorf and Sealy (1994) reported that redwings that incubated overnight were significantly more likely to be present at their nests when cowbirds arrived in the morning, and these birds spent more time vigilant during this critical time. Overnight nest attentiveness and early morning vigilance can be advantageous for redwings and many other hosts, because cowbirds usually remove a host

egg from parasitized nests (Nolan 1978, Weatherhead 1989, Røskaft et al. 1990, Clotfelter 1998a). Early onset of incubation accelerates nestling development, which helps early hatched offspring compete with parasitic young (Wiley and Wiley 1980). Nest attentiveness and incubation may also protect nests from conspecific brood parasitism and nest interference (Romagnano et al. 1990, Jackson 1993, Beissinger et al. 1998).

For some species, hatching asynchrony may increase fledgling production under certain environmental conditions, but this was not the case in our study of Red-winged Blackbirds. Indeed, the widespread distribution of asynchronous hatching among many birds still requires a satisfactory explanation (Clark and Wilson 1981, Stenning 1996). In our population of redwings, early initiation of nocturnal incubation appeared to facilitate nest defense against Brown-headed Cowbirds. We suggest that in addition to other factors that may select for asynchronous hatching (Forbes et al. 1997), researchers should consider the potential effect of brood parasites on host incubation behavior. Conspecific brood parasitism and nest interference may help to explain the prevalence of asynchronous hatching in species that do not suffer from interspecific parasitism (Beissinger et al. 1998). Our results also highlight the importance of examining within-population variation in incubation behavior and hatching asynchrony (Haftorn 1981, Bortolotti and Wiebe 1993, Harper et al. 1994, Wiebe et al. 1998).

ACKNOWLEDGMENTS

This research was funded in part by an NSF Dissertation Improvement Grant (IBN95-28346) to EDC and an NSF-RUI grant (IBN93-06620) to KY. Logistical support was provided by the McNair Scholars Program of Beloit College. We owe considerable thanks to Larry Diehls and his family for access to Diehls Prairie and to Dick Newsome and The Nature Conservancy for stewardship of Newark Road Prairie. We also thank Cort Griswold, Heather O'Brien, and Linh Tu for outstanding field assistance. Numerous other assistants contributed to the nest records from 1984 to 1996. Richard Stenstrom provided access to temperature and precipitation data. The manuscript was improved by comments from Trond Amundsen, Steve Beissinger, Amy Coulthard, Scott Forbes, Erick Greene, Bonnie Ploger, and Larry Wolf.

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Associate Editor: E. Greene