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PARTIAL INCUBATION AND HATCHING ASYNCHRONY IN THE RED-SHOULDERED HAWK (*BUTEO LINEATUS*)[1]

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Abstract.—Like many raptors, Red-shouldered Hawks (*Buteo lineatus*) exhibit asynchronous hatching, which is thought to be a parental strategy for rearing the maximum number of offspring under conditions of unpredictable prey availability. Current knowledge of incubation patterns and the associated behavioral mechanisms by which asynchronous hatching occurs in raptors is limited, and few detailed quantitative studies are available for any species of Accipitriformes. We investigated the effects of egg-laying intervals and parental behavioral incubation patterns during egg-laying on hatching asynchrony in the Red-shouldered Hawk. We used 24-hr/d digital color/infrared video cameras at 15 Red-shouldered Hawk nests to record egg-laying and hatching, and to quantify the proportion of time parents spent incubating, standing, or absent from the nest. The mean egg-laying interval was 2.9 ± 0.1 d or 69.8 ± 2.2 hr (range = 65.8–74.2 hr), and the mean duration of incubation (from the onset of full incubation to hatch) for last-laid eggs was 33 d (32–34 d, $n = 15$). Red-shouldered Hawks exhibited partial incubation behavior, with the delay in the onset of full incubation varying by clutch size and among individuals; full incubation generally began with or just after the laying of the penultimate egg of the clutch. The mean interval between the hatching of the first and second egg was 0.56 ± 0.49 d; between the second and third eggs, 1.24 ± 0.71 d ($P = 0.0215$); and between the third and fourth eggs, 2.42 ± 0.38 d ($P < 0.0004$). The total amount of time parents at each nest spent incubating during the egg-laying period explained most of the variation in the amount of time between the hatching of their first and last egg (the hatching span; $r^2 = 0.83$, $P < 0.0001$). Hatching patterns were the result of both the egg-laying intervals and the pattern of partial incubation, which may represent an adaptive mechanism to reduce the hatching interval while maintaining the hatching asynchrony.

Key Words: *Red-shouldered Hawk*; Buteo lineatus; *asynchronous hatching*; *behavior*; *clutch size*; *hatching asynchrony*; *incubation*; *partial incubation.*

INCUBACIÓN PARCIAL Y ECLOSIÓN ASINCRÓNICA EN *BUTEO LINEATUS*

Resumen.—Como muchas rapaces, *Buteo lineatus* muestra eclosión asincrónica, que se considera una estrategia parental para criar el máximo número de polluelos bajo condiciones de disponibilidad impredecible de presas. El conocimiento actual de los patrones de incubación y de los mecanismos de comportamiento asociados por los cuales ocurre la eclosión asincrónica en las rapaces es limitado y pocos estudios cuantitativos detallados están disponibles para cualquier especie de Accipitriformes. Investigamos los efectos del intervalo en la puesta y de los patrones parentales de comportamiento de incubación durante la puesta sobre la asincronía de eclosión en *B. lineatus*. Usamos videocámaras digitales a color equipadas con luces infrarrojas durante 24 horas al día en 15 nidos de *B. lineatus* para registrar la puesta y la eclosión, y para cuantificar la proporción de tiempo que los progenitores invierten incubando, estando presentes o ausentes del nido. El intervalo medio de puesta fue de 2.9 ± 0.1 días o 69.8 ± 2.2 horas (rango = 65.8–74.2 horas), y la duración media de incubación (desde el inicio de la incubación completa hasta la eclosión) para los últimos

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huevos puestos fue de 33 días (32–34 días, $n = 15$). *B. lineatus* exhibió un comportamiento de incubación parcial, con un retraso en el inicio de la incubación completa variando por tamaño de la nidada y entre individuos; la incubación completa generalmente empezó con o justo después de la puesta del penúltimo huevo de la nidada. El intervalo medio entre la eclosión del primer y segundo huevo fue de 0.56 ± 0.49 días; entre el segundo y tercer huevo fue de 1.24 ± 0.71 días ($P = 0.0215$); y entre el tercer y cuarto huevo fue de 2.42 ± 0.38 días ($P < 0.0004$). La cantidad total de tiempo que los progenitores invirtieron incubando en cada nido durante el período de puesta de huevos explicó la mayoría de la variación en la cantidad de tiempo entre la eclosión del primer y último huevo (el período de eclosión; $r^2 = 0.83$, $P < 0.0001$). Los patrones de eclosión fueron el resultado de los intervalos de puesta y del patrón de incubación parcial, que puede representar un mecanismo adaptativo para reducir el tiempo de eclosión mientras se mantiene la asincronía de eclosión.

[Traducción del equipo editorial]

INTRODUCTION

Raptors typically exhibit asynchronous hatching (Newton 1979), the extent of which is determined in part by the egg-laying interval and the timing of the onset of incubation. Full incubation has been variably defined, but the term generally refers to the intensity of incubation achieved after clutch completion, either when parental incubation behavior becomes constant, or when incubation results in egg temperatures that allow embryo development (Wang and Beissinger 2011, Podlas and Richner 2013). However, parents may exhibit partial incubation before clutch completion (Clark and Wilson 1981, Wang and Beissinger 2011). Partial incubation describes a behavioral pattern in which parents spend a lesser proportion of time sitting on and warming their eggs before clutch completion than they do after clutch completion (Wang and Beissinger 2011). This pattern may also be termed “delayed onset of incubation” (Rebstock and Boersma 2011). Partial incubation behavior affects the asynchronous hatching interval and results in eggs hatching at shorter intervals than the egg-laying intervals (Rebstock and Boersma 2011, Wang and Beissinger 2011, Johnson et al. 2013). Current knowledge of the incubation patterns and associated behavioral mechanisms by which asynchronous hatching occurs in raptors is limited, and few detailed quantitative studies are available for any species of the Accipitriformes.

Asynchronous hatching results in a size hierarchy among nestlings, with the first-hatched, senior nestling being larger and the later-hatched, junior siblings progressively smaller. This disparity in nestling size typically favors the senior nestling, in terms of size and/or strength (Hahn 1981). The senior nestling may have a competitive advantage over its siblings, such as a superior ability to acquire food from parents or to physically dominate siblings in aggressive interactions (O’Connor 1978, Mock 1984). Such competition may ultimately result in brood reduction by starvation or siblicide (Stinson 1979). Aggression and competition among nestlings, with varying degrees of severity, is relatively common among birds, including raptors: Black Kite (*Milvus migrans*; Viñuela 1997), Golden Eagle (*Aquila chrysaetos*; Edwards and Collopy 1983), Lesser Spotted Eagle (*Aquila pomerania*; Meyburg 1974), Northern Goshawk (*Accipiter gentilis*; Boal and Bacorn 1994, Estes et al. 1999), Osprey (*Pandion haliaetus*; Poole 1982, Jamieson et al. 1983, Forbes 1991, McLean and Byrd 1991), Red-tailed Hawk (*Buteo jamaicensis*; Stinson 1980), and Spanish Imperial Eagle (*Aquila adalberti*; Meyburg 1987).

Different hypotheses attempt to explain how and why asynchronous hatching and the associated nestling size hierarchy and sibling aggression evolved. Lack (1947) hypothesized that asynchronous hatching may have evolved as a parental strategy for rearing the maximum number of offspring possible, given unpredictable food resource availability. When food resources are inadequate, the latest-hatched nestling(s) will starve quickly, thus reducing the brood size to one for which it is possible for the parents to provide sufficient food. However, if food resources are plentiful, the parents will be able to provision all their young with adequate food so that all young survive, regardless of hatch rank (Lack 1954). This idea has become known as the “facultative brood reduction hypothesis” and more specifically, the “food amount hypothesis” (Mock et al. 1987). A brood may be reduced as a direct result of starvation, or by siblicide as a proximate result of an insufficient amount of food. In the Blue-footed Booby (*Sula nebouxii*), aggression among siblings was triggered by experimental food deprivation (Drummond and Chavelas 1989). Similarly, brood reductions related to feeding rates or food shortages occur in the Northern Goshawk (Estes et al. 1999), Osprey (McLean and Byrd 1991, Steidl and Griffin 1991), Swainson's Hawk (*Buteo swainsoni*; Bechard 1983), and Boreal Owl (*Aegolius funereus*; Valkama et al. 2002). Recent phylogenetic comparative analyses of 65 Accipitrid raptor species found that the intensity of sibling aggression increases in species with smaller clutch sizes and lower rates of parental food provision, which are indicative of a species' slow life history pace (high adult survival and lower parental effort; Redondo et al. 2019).

Hatching asynchrony occurs in the Red-shouldered Hawk (*Buteo lineatus*; Bent 1937), a medium-sized raptor that typically inhabits forested environments, particularly near riparian and wetland areas (Bednarz and Dinsmore 1982, Morris and Lemon 1983, Woodrey 1986, Howell and Chapman 1997), or urban/suburban areas that are partially forested or adjacent to intact forests (Bloom and McCrary 1996, Dykstra et al. 2000, Wheeler 2003). Although asynchronous hatching (Bent 1937) and sibling aggression (Townsend 2006) have been reported, the behavioral mechanisms driving asynchronous hatching, the egg-laying intervals, and the hatching intervals remain unknown. Therefore, we aimed to investigate the relationship between parental incubation patterns during egg-laying and hatching asynchrony. Specifically, our objectives were to (1) quantify the egg-laying intervals, (2) quantify the amount of time the parents spend incubating during the day and night throughout the egg-laying period, (3) quantify hatching intervals, and (4) determine the effects of the egg-laying interval and parental incubation behavior during the egg-laying period on the hatching asynchrony of the Red-shouldered Hawk.

METHODS

Study Area. Our study area includes parts of Hamilton, Clermont, and Warren Counties that comprise a swath of suburban development surrounding the city of Cincinnati, Ohio, USA. This hilly, unglaciated area in the Interior Plateau ecoregion as defined by Omernik (1987) and Ohio Environmental Protection Agency (Larsen et al. 1988) is partitioned by several ravines and valleys with small streams and two large rivers, the Great Miami River and the Little Miami River. The native upland forest composition is characterized by second-growth oak-hickory (*Quercus* spp., *Carya* spp.) and beech-maple (*Fagus grandifolia*, *Acer saccharum*) associations. The bottomland riparian forest is dominated by American sycamores (*Platanus occidentalis*) and beech. The elevation ranges from approximately 140 to 270 m.

Suburban portions of the study area vary from densely populated (residential lots approximately 20 × 35 m) to sparsely populated (>2.5-ha residential lots, as well as undeveloped private land; Dykstra et al. 2000). Several nest trees are located in private yards of residences and other buildings with nonnative vegetation, but with nearby steep slopes or riparian areas with native vegetation. Other nonresidential portions of the study area include heavily used recreational lands (Dykstra et al. 2000).

Red-shouldered Hawks in the study area begin courtship in February, followed by nest-building or refurbishing, with egg-laying from mid-March to mid-April (mean date of 23 March; Dykstra et al. 2020, C. Dykstra unpubl. data). Clutch size for the species typically ranges from 2 to 4 eggs (Portnoy and Dodge 1979, Townsend 2006). Incubation lasts about 33 d per egg (Palmer 1988) and the eggs hatch asynchronously (Bent 1937).

Nest Location and Installation of Video Cameras. We visited previously known Red-shouldered Hawk territories (Dykstra et al. 2000, 2009) from mid-February until the end of March to locate nests and determine occupancy. We considered a nest occupied if it had been improved with fresh sticks or green vegetation (Dykstra et al. 2000).

To facilitate continuous monitoring, we deployed video cameras at selected occupied nests before the hawks laid eggs (most sites), or where the hawks had laid only a single egg (two sites). We selected the nests based on ease of access for climbers and permission from landowners. All nests studied were located in trees on private land. We mounted cameras between 7–22 March 2011 and 28 February–14 March 2012.

The digital video monitoring systems comprised a 24-hr high-resolution time-lapse color/infrared video camera and a mini digital video recorder (MDVR; model AKR-200, Seorim Technology Co., Ltd., Seoul, South Korea; model MDVR14-4, Supercircuits, Austin, TX, USA) with a 32-GB SDHC memory card. The system was connected with a 30.5-m BNC-to-BNC cable (model CAB-BNC-100, Supercircuits, Austin, TX, USA) and powered by one 12-volt deep-cycle marine battery. We used a 17.8-cm handheld video monitor (Haier model HLT 71) to ensure correct viewing angle and focus of the camera during installation, and to check the nest on follow-up visits. Ro-pel animal and rodent repellent (Burlington Scientific, Farmingdale, NY, USA) was applied to the cables to discourage chewing by mammals such as eastern gray squirrels (*Sciurus carolinensis*).

We employed two different types of cameras in these video recording systems. The close-range camera system consisted of a weatherproof, high-resolution time-lapse color/infrared security video camera (model PC177IRHR-8, Supercircuits, Austin, TX, USA) mounted approximately 0.4–0.6 m above a nest. The far-range camera system was employed at nests where mounting the camera at close range was not easily feasible, and used a weatherproof, variable-distance focus, high-resolution time-lapse color/infrared security video camera (model PC8017IR, Supercircuits, Austin, TX, USA) mounted approximately 2 m from the nest.

Prior to installation, we camouflaged each camera individually to resemble the specific targeted nest tree, using spray paint and bark. The video/power cable was secured to the tree trunk from the nest down to near the ground with IDEAL 19-mm plastic insulated cable staples, then strung at a height of approximately 2 m above the ground to an adjacent tree approximately 8–15 m from the nest tree. We placed a camouflaged, waterproof, 53-L plastic bin containing the MDVR and battery at the base of this adjacent tree to reduce disturbance directly under the nest tree itself. Video was recorded by the MDVR in high quality, at a rate of 10 or 15 frames per sec, with a 704 × 480 resolution. We visited each camera nest every 3 d to check its status and exchange the memory card and battery, and removed the cameras after nest failure or after nestlings fledged.

Video Review and Analysis. SJM reviewed video recordings for each nest from the time the first egg was laid to morning civil twilight the night after the last egg was laid. The dates and times of laying were recorded, except that laying times for two eggs were not recorded due to camera malfunction, and two eggs were already in the nest during camera installation. We classified adult behavior as "standing," "incubating," or "absent," and recorded the date, start and end times, and duration of each bout of behavior, as well as the sex of the parent bird (based on differences in the tail band patterns of each bird, with the female identified during egg-laying). We classified each bout by its occurrence in either day or night according to morning and evening civil twilight for each date, following Wang and Beissinger (2009). We calculated the proportion of day and night that birds spent exhibiting each of these three behaviors.

Where possible, we recorded exact hatching times for each egg. Precise hatching times of some eggs were difficult to determine, as they hatched while the female was incubating or brooding and thus blocking the view from the video camera. Therefore, for these eggs we recorded the interval of time between the last time the intact egg was visible and the first time the hatched nestling was visible. Based on the appearance of the newly hatched nestling (wet or dry with fluffy down), we then estimated the hour in which each egg likely hatched during the time interval recorded for possible hatching. We estimated the hatching intervals within each nest to the nearest 0.25 d. Because the last egg in a clutch was always fully incubated from the time that it was laid until the time it hatched, we also determined the minimum duration of incubation required to hatch an egg.

We defined the "egg-laying interval" as the amount of time between the laying of one egg and the subsequent one, and the "hatching interval" as the amount of time between the hatching of one egg and the subsequent one. We further defined "hatching span" as the amount of time (in d) between the hatching of the first egg and the hatching of the last egg, and the "total amount of incubation time prior to clutch completion" as the sum of all the hours parents spent incubating eggs from the laying of the first egg until the laying of the last egg.

To define "full incubation" for the birds in this study, we quantified the proportion of time spent incubating in mid-incubation by randomly selecting one day that was at least 7 d after clutch completion and 7 d before hatching for each nest and calculating the proportion of time parents spent incubating during one full day and night. Using a modified method suggested by Wang and Beissinger (2011), we calculated the lower limit of the 90% CI of the mean proportion of time (daytime and nighttime) that parents from all nests spent incubating after clutch completion. We then used these lower 90% CI values as thresholds to identify full incubation; any day or night with incubation time greater than the appropriate threshold value was classified as having full incubation. We aligned egg-laying dates with incubation patterns for each nest to determine the onset of full incubation relative to egg-laying. We plotted incubation patterns over time for each nest as the percentage of time eggs were

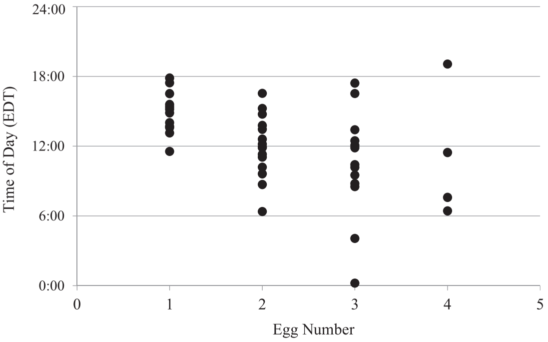

Figure 1. Time of day (Eastern Daylight Time) that 44 eggs were laid in 15 Red-shouldered Hawk nests in Cincinnati, Ohio, 2011 and 2012, with respect to egg number. Due to the length of the egg-laying interval, successive eggs were often laid earlier and earlier in the day.

incubated during days, nights, and 24-hr periods. We summarized these by clutch size as mean ± SE. We also characterized each pattern of incubation according to the classifications outlined by Wang and Beissinger (2011): W-shaped, U-shaped, flat-rise, slow-rise, rapid-rise, pulsed, or irregular.

Statistical Analyses. We used a linear model in R (version 2.15.3, R Development Core Team 2013, function lm) to test for an effect of clutch size on hatching interval, and then used ANOVA in SAS / STAT® software (version 9.2, SAS Institute 2008) to test for differences among hatch intervals. We used a one-tailed *t*-test in SAS to test for differences in mean egg-laying and hatching intervals (in hr), as we would not expect the hatching intervals to be longer than the laying intervals. To determine how the amount of incubation prior to clutch completion influences the hatching span, we used a paired *t*-test to determine if there was a significant difference between the total amount of incubation time prior to clutch completion and the hatching span, and used linear regression to analyze the relationship of these two variables.

RESULTS

Timing of Egg-laying. We mounted cameras at five occupied nests in 2011 and 10 occupied nests in 2012. Two of these nests each had a single egg already present during camera installation. Red-shouldered Hawks laid eggs at all 15 nests after camera installation, and we recorded parental behavior during the egg-laying period at all 15 nests. One nest held a 2-egg clutch, ten had 3-egg clutches, and four had 4-egg clutches, for a total of 48 eggs. The precise dates and times of laying were recorded for 44 of the 48 eggs (Fig. 1).

Overall, the interval between the laying of one egg and the subsequent egg in that nest averaged 2.9 ± 0.09 d or 69.8 ± 2.2 hr (range = 65.8–74.2 hr; $n = 28$ intervals). Most eggs were laid during the daytime, between 0600 H and 1800 H (Eastern Daylight Time, $n = 41$), and of these, 23 eggs (56.1%) were laid in the afternoon and 18 eggs (43.9%) were laid in the morning (Fig. 1). First eggs were most often laid in the afternoon ($n = 11$) as opposed to the morning ($n = 1$). Due to the length of the egg-laying interval (69.8 ± 2.2 hr), successive eggs were typically laid progressively earlier in the day (Fig. 1).

Incubation During Egg-laying. Female parents were the primary incubators, accounting for a mean of 90.8% of the total incubation time during the egg-laying period (range = 76.4–99.2%; $n = 15$ nests). The mean proportion of time spent incubating during the mid-incubation period was 96.1% in the daytime, with a lower limit of the 90% CI of 94.4%. The mean proportion of time spent incubating during the nighttime for all nests was 99.3%, with a lower limit of the 90% CI of 98.7%. We used these daytime and nighttime 90% lower CI values as the thresholds to define full incubation.

The onset of full incubation varied among nests (Fig. 2). For the only 2-egg clutch (Tanager Hills nest), full incubation began the night before the second (ultimate) egg was laid (Fig. 2, 3). For six of the ten 3-egg clutches, full incubation began after the second egg and before the third egg was laid (Clough, Murdoch, Whalen, Paxton, Sweetbriar, and Velma nests). For three of the ten 3-egg clutches, full incubation was not achieved until after clutch completion (Adams, Grandview, and Raintree nests). For one of the ten 3-egg clutches (Linton nest), full incubation was achieved on the first night after the first egg was laid, but was otherwise variable throughout the egg-laying period (Fig. 2, 4, Supplemental Fig. S1). In the four 4-egg clutches, full incubation began between the third and fourth eggs for two nests (Barre and Retswood nests) and with or after the laying of the fourth egg for two nests (Harrison-Grog and Snider nests; Fig. 2, 5, Supplemental Fig. S2).

Following Wang and Beissinger's (2011) classification system, daytime incubation patterns included the following: W-shaped ($n = 3$), U-shaped ($n = 3$), slow-rise ($n = 2$), pulsed ($n = 3$), and irregular ($n = 1$). Nighttime incubation patterns included: flat-rise ($n = 5$), W-shaped ($n = 2$), pulsed ($n = 2$), rapid-rise

Eggs Laid	**1**						**2**						**3**						**4**	
Day or Night	**D 1**	**N 1**	**D 2**	**N 2**	**D 3**	**N 3**	**D 4**	**N 4**	**D 5**	**N 5**	**D 6**	**N 6**	**D 7**	**N 7**	**D 8**	**N 8**	**D 9**	**N 9**	**D 10**	**N 10**
Tanager Hills						X	X	X												
Linton		X				X				X		X		X						
Clough											X		X	X						
Murdoch												X		X						
Whalen	▨	▨	▨	▨							X			X						
Sweetbriar												X		X						
Paxton								X		X		X		X						
Velma												X	X	X						
Adams																				
Raintree	▨	▨	▨	▨																
Grandview														X						
Barre								X			▨	▨	X	X	X	X	X	X	X	X
Retswood																X		X		X
Snider																			X	X
Harrison-Grog	▨	▨	▨	▨																

Figure 2. The onset of full incubation during egg-laying at 15 Red-shouldered Hawk nests in Cincinnati, Ohio, 2011 and 2012, as determined by the lower limit of the 90% CI values of daytime and nighttime full incubation. An "X" represents a day or night in which full incubation was achieved. Shaded boxes indicate a lack of video data. Final clutch size was 2 eggs for Tanager Hills, 3 eggs for Linton, Clough, Murdoch, Whalen, Sweetbriar, Paxton, Velma, Adams, Raintree, and Grandview, and 4 eggs for Barre, Retswood, Snider, and Harrison-Grog.

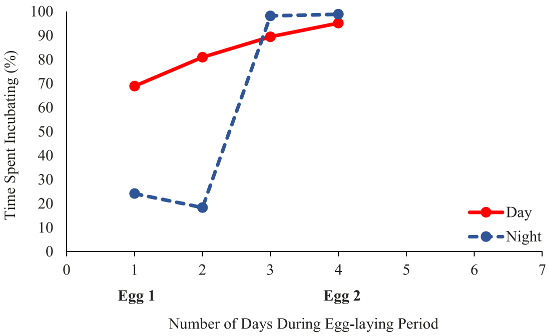

Figure 3. Daytime and nighttime incubation during egg-laying at the Tanager Hills Red-shouldered Hawk nest, the only 2-egg clutch, with full incubation achieved on Night 3, in Cincinnati, Ohio, 2011. The day the first egg was laid was designated as Day 1; the second egg was laid on Day 4.

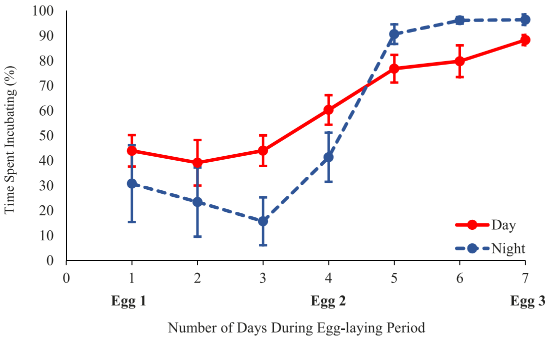

Figure 4. Daytime and nighttime incubation (mean ± SE) during egg-laying at 10 Red-shouldered Hawk nests with 3-egg clutches in Cincinnati, Ohio, 2011 and 2012. Two nests lacked data for the first two days and nights. The day the first egg was laid was designated as Day 1; on average, the second egg was laid on Day 4, and the third on Day 7.

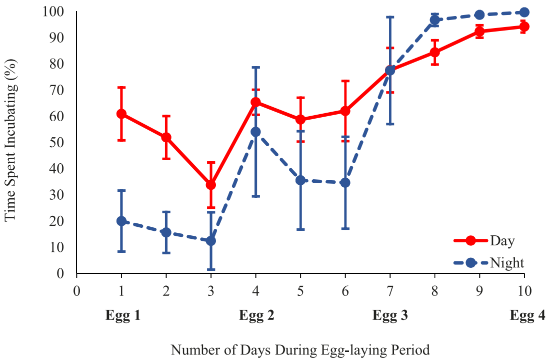

Figure 5. Daytime and nighttime incubation (mean ± SE) during egg-laying at four Red-shouldered Hawk nests with 4-egg clutches in Cincinnati, Ohio, 2011 and 2012. One nest lacked data for day and night 6; another nest lacked data for the first two days and nights. The day the first egg was laid was designated as Day 1; on average, the second egg was laid on Day 4, the third on Day 7, and the fourth on Day 10.

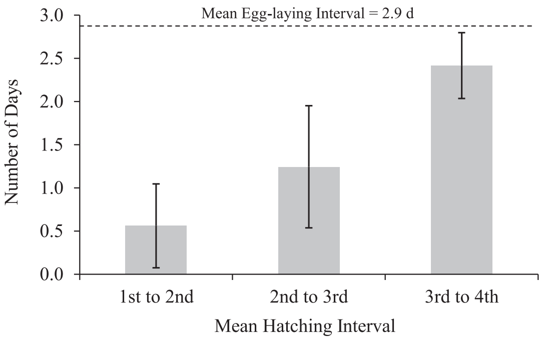

Figure 6. Mean (±SD) hatching intervals at 11 Red-shouldered Hawk nests, in Cincinnati, Ohio, 2011 and 2012. The mean egg-laying interval (for all pairs of eggs) is shown as a dashed line at 2.9 d.

($n = 1$), U-shaped ($n = 1$), and irregular ($n = 1$). Patterns could not be classified at three nests due to incomplete recordings.

Hatching. At the 15 nests where we recorded behavior, eggs hatched in 12 nests, a total of 35 of the 48 eggs laid (72.9%). One of these 12 nests experienced partial hatching failure, in which only one of three eggs hatched, so this nest (Adams) was excluded from the calculation of hatching intervals. At the Retswood nest, three eggs of the 4-egg clutch hatched, but the first-laid egg failed to hatch, likely due to exposure to freezing temperatures during which time the egg was not incubated (Miller 2013). Eggs in the other three nests failed to hatch due to depredation of the female parent by a Great Horned Owl (*Bubo virginianus*) at the Harrison-Grog nest (4 eggs), disturbance from an eastern gray squirrel at the Clough nest (3 eggs), and the unexplained disappearance of the female parent at the Linton nest (3 eggs; see Miller et al. 2015 for details). We recorded exact hatching times for 23 of the 35 hatched eggs, and estimated the hour in which each of the remaining 12 eggs likely hatched, as the view of these was obstructed by the female parent during hatching. We estimated the hatching intervals within each nest to the nearest 0.25 d. There was no significant effect of clutch size on hatching interval ($P = 0.5333$), so we pooled data across all nests ($n = 11$). The mean hatching interval between the first and second eggs (0.56 ± 0.49 [SD] d, $n = 10$) was significantly less than both the interval between the second and third eggs (1.24 ± 0.71 d, $n = 10$; ANOVA, $P = 0.0215$), and that between the third and fourth eggs (2.42 ± 0.38 d, $P < 0.0004$, $n = 3$; Fig. 6). The mean hatching interval between the second and third eggs was also significantly less than that of the third and fourth eggs ($P = 0.0208$; Fig. 6). These estimations of hatching intervals indicated that eggs hatched with an overall mean of 1.1 ± 0.83 d (26.4 ± 20.0 hr) between eggs, which was shorter than the mean egg-laying interval of 2.9 ± 0.09 d or 69.8 ± 2.2 hr (one-tailed *t*-test; $n = 28$ egg-laying intervals and $n = 23$ hatching intervals, $t = -10.38$, $P < 0.0001$).

The total incubation time prior to clutch completion was positively correlated with the hatching span ($y = 0.838x - 0.192$, y = hatching span, x = total incubation time prior to clutch completion, both in days; $n = 11$ nests, $r^2 = 0.83$, $P = < 0.0001$; Fig. 7). Generally, total incubation time prior to clutch completion ($\bar{x} = 2.98 \pm 1.15$ d) was longer than the mean hatching span (2.31 ± 1.06 d; $n = 11$ nests, $P = 0.0008$). We also calculated the number of days between the laying and the hatching of the last egg and found that the mean duration of incubation of each last egg was 33 d (range: 32–34 d, $n = 12$).

DISCUSSION

We found that Red-shouldered Hawks exhibit partial incubation during the egg-laying period, with a delay in the onset of full incubation. As a result, hatching intervals are shorter than the egg-laying intervals, particularly between the older siblings. The egg-laying intervals, partial incubation, and the

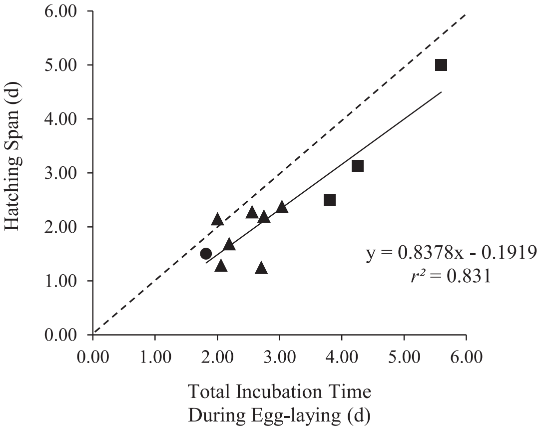

Figure 7. Correlation between the total incubation time prior to clutch completion and the hatching span (time between the first and last egg) for 11 clutches in Red-shouldered Hawk nests in Cincinnati, Ohio, 2011 and 2012. The dashed line represents a perfect correlation between hatching span and total incubation time prior to clutch completion, and the solid trend line shows the actual relationship between hatching span and total incubation time prior to clutch completion. The circle marker indicates the 2-egg clutch, triangles indicate 3-egg clutches, and squares indicate 4-egg clutches.

timing of the onset of full incubation all contribute to the asynchronous hatching patterns observed.

Egg-laying. Ours is the first study to quantify the Red-shouldered Hawk's egg-laying intervals ($\bar{x} = 69.8 \pm 2.2$ hr) using video technology. Researchers in Wisconsin approximated the laying interval for Red-shouldered Hawks as ca. 50 hr, but further information about methods or the accuracy of this quantification was not provided (E. Jacobs in Dykstra et al. 2020). The duration of the incubation period that we documented (x = 33 d, range = 32–34 d) was consistent with earlier information reported by Palmer (1988). Our study is one of few to report the time of day for egg-laying in the Accipitridae, and the first to do so for the Red-shouldered Hawk. The egg-laying interval and the resulting time of day for egg-laying may have evolutionary adaptive importance for ensuring that all eggs are laid during daylight hours, perhaps to avoid depredation of the laying female by nocturnal predators such as the Great Horned Owl or raccoon (*Procyon lotor*). Interestingly, the only female parent that was killed during the incubation period (by a Great Horned Owl; see Miller et al. 2015) was also the only one to have laid an egg in the middle of the night (Harrison-Grog nest, Fig. 2).

Incubation Behavior. Few researchers have accurately quantified the incubation behavior of parent birds, the pattern of partial versus full incubation, and the resultant hatching asynchrony for any species of the order Accipitriformes. Bortolotti and Wiebe (1993) used an electronic balance to quantify diurnal nest attendance by male and female American Kestrels (*Falco sparverius*), and also estimated the time of egg-laying, but did not record nocturnal attendance. They observed a drastic increase in the percent occupancy of the nest boxes from the time the penultimate egg was laid ($n = 4$ breeding pairs). Unfortunately, each of these four pairs experienced some degree of hatching failure, so the researchers were unable to determine the relationships between partial incubation and the hatching pattern. Similarly, Wiebe et al. (1998) documented intraspecific variation in incubation patterns of the Eurasian Kestrel (*Falco tinnunculus*) by using temperature loggers in the nest cup to quantify incubation during egg-laying. Like Bortolotti and Wiebe's (1993) findings on American Kestrels, this study also found that females typically achieved full incubation on the day or the day after the penultimate egg was laid, although four of seventeen did not achieve full incubation until the day after clutch completion ($n = 17$ nests). The pattern of the onset of incubation during egg-laying varied widely among individual female parents. Like American Kestrels (Bortolotti and Wiebe 1993) and Eurasian Kestrels (Wiebe et al. 1998; order Falconiformes), the Red-shouldered Hawk also exhibits considerable variation among individuals in incubation patterns and the timing of the onset of full incubation during egg-laying. Part of this variation may be attributed to differences in clutch size. In general, we found that the onset of full incubation occurs with or just after the laying of the penultimate egg. However, there was also some variation among nests with the same clutch size. A few nests with 3-egg clutches achieved full incubation on the first or third egg rather than the second, and a few with 4-egg clutches achieved full incubation on the second or fourth egg.

Weather factors, including ambient temperature, precipitation, and wind, may explain some variation in parental incubation behavior during egg-laying (Ardia et al. 2006, Wang and Beissinger 2009, Johnson et al. 2013). In our study, air temperatures may have influenced incubation behavior during egg-laying. The two nests (Paxton and Linton) where hawks approached or achieved full incubation at the beginning of egg-laying experienced isolated events of near- or below-freezing overnight ambient temperatures at the beginning of egg-laying (Miller 2013), which may explain their earlier onset of full incubation (Fig. 2, Supplemental Figure S1). However, the same did not occur at the Barre and Retswood nests (Fig. 2, Supplemental Figure S2), at which hawks approached or achieved full incubation earlier than expected (the night after the second egg was laid in a clutch of four eggs), when ambient temperatures were not near freezing. Therefore, a premature onset of incubation of earlier eggs may only be partially explained by low ambient temperature. In addition, the hatching failure of the first egg at the Retswood nest was likely due to exposure to freezing temperatures that occurred the second night after it was laid, when the parents were inexplicably absent overnight.

Individual Variation in Incubation Behavior. Although we did not observe multiple nesting periods for the same individual females, it is possible that differences in behavioral incubation patterns may be attributed to intrinsic differences across females. Variation in the onset of incubation irrespective of clutch size has been documented in the Ural Owl (*Strix uralensis*), in which 25% of the variation is explained by repeatable differences across females (Kontiainen et al. 2010). Variability in incubation patterns among individuals is also reported for non-raptors (Johnson et al. 2013). Although weather may be a large influence on incubation behavior, factors such as female condition and prey availability may also play a role (Wiebe et al. 1998, Sockman et al. 2006, Johnson et al. 2013).

Although the characterization of incubation patterns according to Wang and Beissinger's (2011) classification system revealed variability among individual nesting pairs, the flat-rise pattern for nocturnal incubation was the most common, which may indicate that nocturnal behavior can better serve as an identifier of the timing of the onset of full incubation, as the nocturnal behavior was less variable than diurnal behavior at each nest. In some non-raptor species, females achieve full incubation at night well before reaching full incubation during the daytime (Martin et al. 2007, Wang and Beissinger 2009).

Influence of Incubation Behavior on Hatching Intervals and Asynchrony. Red-shouldered Hawks' delay in the onset of full incubation resulted in shorter hatching intervals between the earliest eggs, thereby reducing hatching asynchrony relative to the egg-laying intervals (Fig. 6). The amount of time spent incubating prior to the laying of the last egg was closely related to the hatching span, explaining 83% of the variation in the hatching span in our study. In a similar study of Eurasian Kestrels, the amount of incubation during egg-laying explained 91% of the variation in hatching span (Wiebe et al. 1998). If incubation were continuous from the time of the onset of full incubation, we might expect a perfect correspondence between hatching span and the amount of incubation time prior to clutch completion. However, in our study, the total incubation time prior to the laying of the last egg was actually slightly greater than the hatching span (Fig. 7). One possible explanation for this is that the cumulative amount of incubation behavior does not translate exactly to embryo development. Although parents exhibited incubation behavior, the eggs were not necessarily reaching optimal incubation temperatures (35–38°C; Webb 1987). Instead, some incubation behavior may have served to simply maintain egg viability above freezing temperatures, but below physiological zero (24–28°C; Webb 1987), at which temperature embryo development begins. In some non-raptor species, incubation behavior without heat transfer to the eggs may serve other functions, such as deterring predators or nest competitors (Podlas and Richner 2013, Wiebe and Martin 1998).

Camera Methodology. Our study's methodology allowed us to assess the efficacy of installing nest cameras prior to the egg-laying period (or when only one egg had been laid). This technique allowed us to obtain valuable data on egg-laying, hatching, and incubation behavior, and did not induce disturbance at the nests of suburban Red-shouldered Hawks. Pairs laid eggs at all 15 nests where we installed cameras during the courtship/early egg-laying period of the breeding cycle. Such uniform acceptance of the camera did not occur when we mounted cameras during the first or second week of the nestling phase; of 11 such cameras, one had to be removed because of aberrant parental behavior (e.g., hawk would not enter the nest; Miller 2013). Thus, mounting cameras early was the more conservative, less-disruptive option. In addition, if hawks had rejected a nest with an installed camera, they could have built a replacement nest elsewhere in their territory in as little as 1–2 wk (C. Dykstra unpubl. data). Such easy acceptance of cameras may be related to these suburban birds' tolerance of disturbance (Dykstra et al. 2018) however, and is not necessarily expected of other raptor species, particularly those nesting in more remote environments. Post-installation monitoring of nests with cameras is always appropriate to minimize researcher disturbance (Harrison et al. 2019).

Conclusions. In summary, Red-shouldered Hawks exhibit partial incubation during the egg-laying period, with a delay in the onset of full incubation varying with clutch size and individual parent behavior. Asynchronous hatching patterns are the result of the egg-laying intervals, the pattern of partial incubation, and the timing of the onset of full incubation. This behavior is likely an adaptive mechanism to reduce the hatching interval while maintaining the asynchronous pattern. Our results may improve our understanding of the establishment of nestling size hierarchies and related sibling behavior.

SUPPLEMENTAL MATERIALS (available online). Supplemental Figure S1: Incubation behavior (24-hr) during egg-laying at 10 Red-shouldered Hawk nests with 3-egg clutches in Cincinnati, Ohio, 2011 and 2012. Figure S2: Incubation behavior (24-hr) during egg-laying at four Red-shouldered Hawk nests with 4-egg clutches in Cincinnati, Ohio, 2011 and 2012.

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