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TEMPORAL CONSTRAINTS ON THE INCIDENCE OF DOUBLE BROODING IN THE LOUISIANA WATERTHRUSH

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Abstract. We studied the nesting of the Louisiana Waterthrush (*Seiurus motacilla*) in western Pennsylvania from 1996 to 2008. Eight of 143 pairs (5.6%) that successfully fledged young from their first nest attempted a second brood, the first cases of double brooding reported for this species. Given the potential for double brooding to increase annual productivity, its infrequency suggests strong costs offsetting this life-history strategy. Molting is a late-season constraint that may influence the occurrence of double brooding in this migratory species. The waterthrushes' nesting season extended from 14 April to 30 July. A single nesting cycle, from clutch initiation through post-fledging care, encompassed 48–55 days. The mean date of clutch initiation for first attempts of single-brooded pairs was 5 May, with at least two thirds of pairs renesting if their first nest attempt failed; the mean date of initiation of second clutches was 25 May. The mean dates of first and second clutches of eight double-brooded pairs were 29 April and 4 June, respectively. The average date of onset of molt was 26 June, and molt was completed in about 40 days, or by early August in most birds. Double-brooded and very late-renesting single-brooded birds delayed molt by up to 3 weeks later than average, and their molt and breeding overlapped by up to 4 weeks. Delayed molt and migration associated with late nesting may be an especially significant cost of double brooding for the Louisiana Waterthrush because it is among the earliest migrants returning to its wintering grounds, where the birds compete strongly for optimum territories.

Key words: *double brooding, Louisiana Waterthrush, mating systems, molt, Neotropical migrant, riparian,* Seiurus motacilla.

Restricciones Temporales sobre la Incidencia de la Anidación Doble en *Seiurus motacilla*

Resumen. Estudiamos la anidación de *Seiurus motacilla* en el oeste de Pensilvania desde 1996 hasta 2008. Ocho de las 143 parejas (5.6%) que criaron juveniles exitosamente en sus primeras nidadas intentaron realizar una segunda nidada. Estos son los primeros casos de anidación doble detectados para esta especie. Dado el potencial que tiene la anidación doble para aumentar la productividad anual, su baja frecuencia sugiere que tiene altos costos que descompensan esta estrategia de vida. La muda es una limitante a finales de la estación que puede influenciar la ocurrencia de anidación doble en esta especie migratoria. La época de anidación de *Seiurus motacilla* se extendió desde el 14 de abril hasta el 30 de julio. Cada ciclo de anidación, desde el inicio de la nidada hasta el cuidado post-emplumamiento, abarcó entre 48 y 55 días. La fecha promedio de inicio de la nidada, para los primeros intentos de las parejas con un solo intento de anidación, fue el 5 de mayo, con al menos dos tercios de las parejas anidando nuevamente si su primer intento de anidación fracasó. La fecha promedio de iniciación de las segundas nidadas fue el 25 de mayo. Las fechas promedio de las primeras y segundas nidadas de ocho parejas con anidación doble fueron el 29 de abril y el 4 de junio, respectivamente. La fecha promedio del comienzo de la muda fue el 26 de junio y la muda se completó en unos 40 días o hasta principios de agosto en la mayoría de las aves. Las aves con anidación doble y con anidación simple que vuelven a nidificar muy tarde retrasaron la muda hasta tres semanas en comparación con el promedio, y sus mudas y la crianza se superpusieron hasta cuatro semanas. El retraso de la muda y de la migración asociado con la anidación tardía puede ser un costo especialmente significativo de la anidación doble para *S. motacilla*, porque esta especie está entre los primeros migrantes que regresan a sus áreas de invernada, donde las aves compiten fuertemente por los mejores territorios.

INTRODUCTION

Life-history strategies of nearctic–neotropical migratory birds have presumably evolved to exploit the seasonal availability of food in temperate regions. Species-specific timing of migration, nesting, and molt should, therefore, be adapted to maximize the annual production and survival of young against future reproductive opportunities of the parents (Lack 1950, Martin 1987). Variation in fecundity from double or multiple brooding carries with it the inherent selective advantage of potentially increasing the annual fecundity of a breeding pair (Geupel and DeSante 1990, Holmes et al.

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1992, Evan-Ogden and Stutchbury 1996, Morrison 1998), so double brooding will affect models describing population growth or stability. Thus, differences within and among species in the occurrence or extent of double brooding have important implications for avian conservation (Nagy and Holmes 2005b). The incidence of double brooding and the factors that determine it, however, remain unclear for most species.

Nearctic–neotropical migrants, including many wood warblers, generally have been described as single brooded, largely on the basis of an assumption of strong temporal constraints (Morse 1989). Detecting double or multiple brooding, however, requires intensive monitoring of color-banded populations, often over several seasons (Holmes et al. 1992). Facultative double brooding actually has been found to be moderately frequent (30–60% of nesting pairs) in a few well-studied wood warbler species (Nolan 1978, Petit 1989, Holmes et al. 1992, Evan-Ogden and Stutchbury 1996), while studies of other species in that family have found no evidence of double brooding (Dececco et al. 2000) or have shown double brooding to be very rare (Zach and Falls 1976, Miller 2003). Factors affecting differences in the frequency or occurrence of double brooding may include length of the breeding season (Holmes 1989, Petit 1989, Monroe et al. 2008), food availability (Holmes et al. 1992, Rodenhouse and Holmes 1992, Nagy and Holmes 2005a, b), and age or experience of the breeding adults (Geupel and DeSante 1990, Holmes et al. 1992), but Evan-Ogden and Stutchbury (1996) and Ligi and Omland (2007) have also proposed that molt and migration schedules may constrain double brooding.

The Louisiana Waterthrush (*Seiurus motacilla*) is among the earliest migrants to return from the Neotropics to temperate breeding grounds, with many individuals arriving in western Pennsylvania by the last week in March (Mulvihill et al. 2008). This very early return and subsequent onset of nesting might be expected to increase the likelihood that this species is frequently double brooded. Previous studies, however, have not found evidence of double brooding (Eaton 1958, Robinson 1995), although Surdick (1996) observed an unsuccessful attempt at what he took to be the same unbanded pair attempting to build a second nest after having fledged one young previously. Previous studies of this species' nesting have been based on observations of fewer than ten pairs so they may not have been expected to detect double brooding if it were not very common.

Our objective in this study was to monitor breeding of the Louisiana Waterthrush intensively to determine the incidence of double brooding in this warbler. To begin to understand what may constrain the waterthrush in this part of its range from double brooding more frequently, we also sought to examine the relationship between the timing of nesting and molting in the species, hypothesizing that double-brooded pairs nest earlier and molt later than single-brooded pairs. Although rarity of occurrence and small sample sizes prevented us from assessing statistically other factors that may mediate the extent of double brooding in the population we studied, we also discuss individual age and breeding experience and food availability as alternative constraints on double brooding in this population.

METHODS

The Louisiana Waterthrush is a riparian specialist that occupies essentially linear territories along forested headwater streams, where it feeds predominantly on aquatic macroinvertebrates (Eaton 1958, Craig 1984). It breeds throughout the eastern United States and winters in Mexico, Central America, and the Caribbean islands. Both sexes help build an open-cup nest on banks, slopes, or in upturned tree roots along streams. Typically only one clutch of five (range: 3–6) eggs is laid, but most birds re-nest if the first attempt fails. Incubation begins upon the laying of the last egg. Only the female incubates, and eggs hatch after a mean 13 days (Robinson 1995, Mulvihill et al. 2008). Nestlings are fed by both parents until ready to fledge at a mean 10 days of age; parents then divide the brood for another 3–4 weeks of post-fledging care (Robinson 1995, Quattrini et al. 2000).

We intensively monitored breeding Louisiana Waterthrushes in western Pennsylvania as part of broader studies of the ecological health of forested headwater streams throughout the state (O'Connell et al. 2003, Mulvihill 2008). Study sites included 2- to 3-km reaches of circumneutral streams (pH ~7), as well as others negatively affected by acid drainage from mines and/or acidic precipitation (pH range 4.5–5.5). Circumneutral streams included Loyalhanna Creek and Powdermill, Phoebe, and Camp runs in Westmoreland County, Roaring and Tressler runs in Somerset County, and Blackberry and Rock runs in Fayette County. Increased acidity was recorded on Laurel, Linn, and Penrod runs in Westmoreland County, Gary's Run in Somerset County, and Jonathan Run in Fayette County. We monitored Laurel Run and Powdermill Run from 1996 to 2008; Linn, Loyalhanna, and Camp runs for five years, 1998–2000 and 2007–2008; Tressler, Mill, Jonathan, and Blackberry for three years, 1998–2000; Rock Run for two years, 1999–2000; and Penrod and Phoebe runs for two years, 2007–2008.

Mixed deciduous forest at our study sites was typical of the mid-Appalachian region, being characterized by beech (*Fagus grandifolia*), red maple (*Acer rubrum*), various oaks (*Quercus* spp.), and yellow poplar (*Liriodendron tulipifera*), with northern hardwoods including eastern hemlock (*Tsuga canadensis*), black birch (*Betula lenta*), and yellow birch (*Betula alleghaniensis*) at some sites. Typical understory species included common spicebush (*Lindera benzoin*), witch hazel (*Hamamelis virginiana*), and striped maple (*Acer pensylvanicum*); the ground cover, where present, was largely dominated by ferns.

We began locating and monitoring Louisiana Waterthrushes soon after their arrival; on some streams the first males returned as early as 23 March. Males were usually captured and banded before they paired by means of territorial-song playback, most females were caught and banded while feeding young at the nest, and nestlings were banded a few days prior to fledging (6–8 days old). Adults were aged as second-year (SY) or after second-year (ASY) on the basis of wing molt limits (Mulvihill 1993). In our population most males (87%), females (70%), and nestlings (93%) were color-banded on study streams each year.

We followed behavior to determine when pairs were nesting and searched for every nest attempt at each site. In monitored territories >90% of nests were found, usually with eggs; extensive search efforts, as well as continuous observation of breeding activity throughout the season, suggest that few, if any, cases of double brooding were missed. Nests were checked at 3- to 4-day intervals for survival of eggs and nestlings. In cases where the clutch-initiation date was not known, it was back-calculated from observed hatching and/or fledging dates, on the basis of an average 13-day incubation (beginning with the last egg laid) and 10-day nestling period (Robinson 1995, Mulvihill et al. 2008). A nesting attempt was considered successful if at least one young was known to have fledged. If fledging was not observed directly, observations of banded fledglings or adults carrying food were used to confirm nesting success.

We determined the extent of double brooding in our population from the number of confirmed cases out of the total number of pairs that successfully fledged young on their first nesting attempt, that is, pairs that might attempt a second brood. To look at the relation of double brooding to the normal nesting chronology of the Louisiana Waterthrush, we compared the timing of nest initiation for first and second nests of double-brooded pairs with first nests of single-brooded pairs and any subsequent re-nesting attempts if the first attempt failed. Because of small samples sizes for double brooding we did not look at annual variation in double brooding or nesting chronology but pooled data from all years. Initiation dates of first nests were normally distributed so we used a two-sample *t*-test to compare the mean date of laying, mean date of fledging, and the number of chicks fledged for first broods of single-brooded pairs and double-brooded pairs.

We looked at potential constraints on double brooding related to timing of the definitive prebasic molt by analyzing molt data from 88 captures of the Louisiana Waterthrush during our study and during routine banding at the Powdermill Avian Research Center from 1986 to 2005. If individuals were scored for molt more than once in the same year, we selected one record at random for statistical analysis. Molt data for the same bird in different years were considered independent records because among those individuals captured in multiple years the date of initiation of molt varied markedly from year to year (see Results).

We used conventional methods for quantifying molt in which each of 18 flight feathers on the right wing are scored 0–5 by their replacement growth (Ginn and Melville 1983). After testing assumptions of normality and homoscedasticity, we followed Pimm (1976) in using a Model I regression to regress date on molt score for males and females, because we were interested in examining the molt schedules and molt rates of individual birds (many with known breeding histories) in our population, not the schedule and timing of molt for the population as a whole. Variation among years was not analyzed; data from all years were combined.

RESULTS

DOUBLE BROODING

We identified eight occurrences of double brooding among 231 first-laid clutches and 82 re-nesting attempts monitored on our study streams (Table 1). In this population, 5.6% (8 of 143) of pairs that successfully fledged young from their first nest were known to attempt a second brood. These represent the first confirmed cases of double brooding for this species and for the genus *Seiurus* (see Discussion). In all but one case both the male and the female of the pair laying the first clutch were also the parents of the second clutch. In the exceptional case ("Penrod 2008"), the female from the first clutch switched mates (and territories) for her second clutch.

NESTING CHRONOLOGY AND SUCCESS

Across all years, the breeding season of the Louisiana Waterthrush was 107 days in length, extending from the earliest clutch initiation on 14 April to the latest observation of provisioning of fledglings on 30 July. Initiation of egg laying in first nesting attempts by 223 single-brooded pairs extended over more than 6 weeks (range: 14 April–1 June), with the mean date of initiation of 5 May (Fig. 1). Out of 231 first nesting attempts by single- and double-brooding pairs with known clutch-initiation dates and outcomes, 51.9% (120 of 231 nests) failed—the vast majority from depredation. Pairs readily renested with 65.8% (79 of 120) known to build a second nest; 38.2% (13 of 34) of these pairs established a third nest and clutch if the second nest failed. The mean date of initiation for second clutches was 25 May (range: 5 May–15 June; Fig. 1); the mean date of initiation of laying for third clutches was 4 June (range: 26 May–14 June; Fig. 1).

The mean date of first clutches of the eight double-brooded pairs was 29 April (range: 14 April–10 May; Fig. 1). The first nest of double-brooded pairs was initiated significantly earlier than the first nest of single brooded pairs (t_{229} = 1.97, $P = 0.02$). The mean date of the second clutch of double-brooded pairs was 4 June (range: 27 May–11 June; Fig. 1).

Fledging followed similar patterns. The mean date of fledging of first broods of single-brooded pairs was 31 May (range: 15 May–27 June; $n = 133$), while the mean fledging date

TABLE 1. Summary of cases of double brooding for Louisiana Waterthrush in Pennsylvania, 1997–2008.

	Powdermill Run 1997	Mill Run 1998	Tressler Run 1999	Camp Run 2000	Roaring Run 2000	Loyalhanna Run 2008 (A)	Loyalhanna Run 2008 (B)	Penrod Run 2008
Male parent age	ASY	ASY	ASY	ASY	ASY	ASY	ASY	ASY/ASY[a]
Female parent age	ASY	ASY	ASY	SY	AHY	unknown	ASY	ASY
Experienced parent[b]	M, F	unknown	M, F	M	M, F_{unk}	M, F_{unk}	M, F_{unk}	M, M, F_{unk}
First brood initiation	10 May	4 May	1 May	30 April	30 April	14 April	26 April	28 April
Fledging date	6 June	31 May	28 May	27 May	27 May	12 May	22 May	27 May
Clutch size/young fledged	5/5	5/5	5/4	4/4	5/5	5/3	5/5	5/5
Second brood initiation	11 June	5 June	3 June	5 June	4 June	27 May	3 June	11 June
Fledging date	6 July	1 July	1 July	depredated	30 June	abandoned	depredated	8 July
Clutch size/young fledged	3/2	4/4	5/5	4/0	5/5	5/0	4/0	4/4
Clutch interval (days)	5	6	6	9	5	15	12	15

[a]Female switched males between first and second broods.
[b]Male (M) or female (F) nested in same territory in previous year(s); unk = unknown.

of re-nesting birds was 18 June (range: 3 June–9 July; $n = 41$). Among double-brooded pairs, the mean fledging date of first broods was 26 May (range: 12 May–6 June; Table 1), and this was significantly earlier than the fledging date of young of single-brooded pairs ($t_{139} = 1.72$, $P = 0.04$). The mean fledging date of second broods of double-brooded pairs was 2 July (range: 30 June–8 July; Table 1).

Five of eight double-brooded pairs were successful in raising a second brood. Pairs attempting two broods averaged 7.0 young fledged (SD = 2.7, $n = 8$) compared to 2.3 young (SD = 2.2, $n = 331$) for all single-brooded pairs, and this difference was significant ($t_{337} = -5.90$, $P < 0.01$). When the comparison was confined to only successful single-brooded pairs, which fledged a mean 4.2 young (SD = 0.9, $n = 182$),

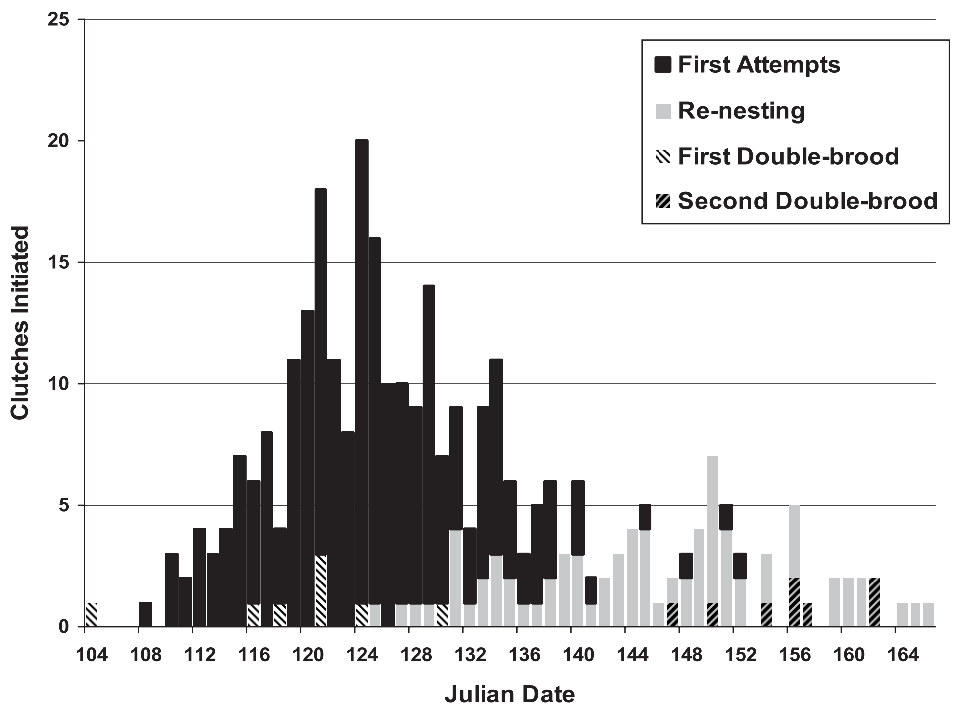

FIGURE 1. Chronology of nest initiation by Louisiana Waterthrushes in Pennsylvania, 1996–2008, for the first nests and replacement nests of single-brooded pairs and first and second nests of double-brooded pairs.

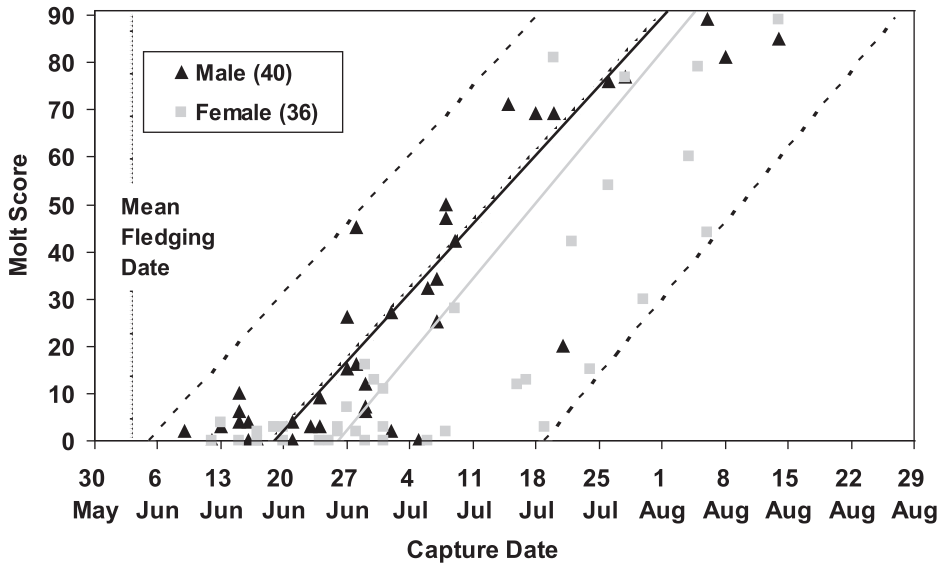

FIGURE 2. Molt chronology of Lousiana Waterthrush in western Pennsylvania 1986–2005 in relation to nesting. A score of 90 indicates a completed molt. Regression lines describe the mean timing and rate of molt for individuals of each sex: black indicates males ($y = 171 + 0.48x$), gray indicates females ($y = 178 + 0.44x$). Dashed lines indicate the timing of molt for the earliest and latest molting individuals.

double-brooded pairs also fledged significantly more chicks ($t_{187} = -5.90$, $P < 0.01$).

EFFECTS OF AGE AND EXPERIENCE

At least 58.9% (10 of 17) of individuals that attempted two broods were experienced breeders returning to the same territory (Table 1). All double-brooded males and most females that were aged were ASY or older. Only a single known SY female was involved in double brooding. No individual waterthrush attempted two broods more than once during our study, even though some nested relatively early and were successful on their first attempt in other years.

TIMING OF MOLT

Molt of adult Louisiana Waterthrushes began over a 5-week period with a mean date of 24 June (range: 12 June–20 July), 3 weeks after the typical fledging date for young of single-brooded pairs, and probably coinciding with juveniles' independence (Fig. 2). Estimated completion of molt was approximately 40 days after the molt's onset, with a mean of 4 Aug (range: 23 July–30 Aug). Molt scores of seven individuals caught in multiple years showed different annual molt schedules that varied by a mean of 10 days (range: 5–27 days), supporting our treatment of molt data for the same bird in different years as independent records. Males initiated and completed molt a mean 8.0 days earlier than females ($F_{1,38} = 11.21$, $P = 0.002$). The sexes molted at generally similar rates of 2.2 molt-score points/day, although females molted at a slightly increased rate that might compensate for delayed onset of molt. On the basis of this rate, the latest molting individuals (including double-brooded birds) would have completed their molt near the end of August, more than 3 weeks after most other birds in the population. This was seen in our capture of several known late breeders observed overlapping molt and care of nestlings and dependent fledglings while still on their breeding territories.

DISCUSSION

This study, based on observations of more than 300 nesting attempts by Louisiana Waterthrushes, provides the first confirmation of double brooding in this species, as well as the first confirmed occurrence of double brooding for the genus *Seiurus.* Male Ovenbirds (*S. aurocapilla*) have twice been observed in association with two nests in the same season (Hann 1937, Zach and Falls 1976); however, in neither case was the female uniquely marked, making it impossible to exclude polygyny as a possible explanation for the observations. We also report here the first case of serial polyandry for the Louisiana Waterthrush. Polygyny has been reported previously from these study sites (Mulvihill et al. 2002), with at least some cases perhaps explained by females' territory fidelity and a locally skewed sex ratio. The case of the polyandrous double-brooding female may also be a result in part of locally skewed sex ratios, as the female nested on a stream where several male waterthrushes failed to attract mates, perhaps as a result of increased stream acidification (Mulvihill et al. 2008).

Though we found multiple examples of double brooding, we demonstrate that its frequency is consistently low, with only about 5% of nesting attempts involving double brooding, and with double brooding observed in fewer than half the years of our study. Double-brooding waterthrushes were able to produce more offspring in a given year, suggesting increased fecundity of the breeding pair, but we caution that we do not know how double brooding may have influenced survival rates of adults or the offspring produced. Given the potential benefit of producing more surviving offspring, however, the low incidence of double brooding in waterthrushes suggests that there are limiting factors and/or offsetting costs to this reproductive strategy.

One of the most obvious potential factors limiting double brooding is the length of the nesting season (Holmes 1989, Petit 1989, Monroe et al. 2008). For species breeding in strongly seasonal environments, the length of a complete nesting cycle largely determines the number of broods that can be raised (Skutch 1976). If the breeding season is relatively short, as for most nearctic–neotropical migrants, timing of the initiation of the first clutch will be a critical factor determining the occurrence of double brooding. Studies of other warblers have found that pairs initiating successful first clutches early in the season were much more likely to attempt second broods (Nolan 1978, Holmes et al. 1992, Evan-Ogden and Stutchbury 1996, Hunt and Eliason 1999).

Because the Louisiana Waterthrush is typically the first warbler to arrive on the breeding grounds in western Pennsylvania (Brauning 1992, Robinson 1995), we might expect double brooding to be frequent in this species. However, despite the Louisiana Waterthrush's early arrival, we found that its breeding season extended over only 107 days from mid-April to the end of July. In the waterthrush's full nesting cycle, clutch initiation typically is followed by 17 days of additional laying and incubation (assuming a clutch size of 5), 10 days of nestling care, and 21–28 days of post-fledging care, for a total 48–55 days devoted directly to reproduction. This is roughly half of the waterthrush's available breeding season, which alone may place severe limits on the possibility of double brooding. This number also suggests that double brooding is restricted to only those pairs whose first successful nests were initiated within a few days of the start of the breeding season.

Our results, though based on a small sample, showed that double-brooded pairs initiated laying of their first clutch significantly earlier (29 April) than did single-brooded pairs (5 May; Fig. 1). Early initiation, however, is clearly not the only requisite for double brooding, as we recorded 16 other successful pairs that initiated clutches prior to 29 April yet did not attempt to lay a second clutch. Thus, although early-season nesting success may be a prerequisite for double brooding, it does not appear to be the only constraint that determines the low incidence of double brooding in the Louisiana Waterthrush.

Age or experience of the breeding adults has been cited as a factor affecting differences in the frequency or occurrence of double brooding (Geupel and DeSante 1990, Holmes et al. 1992). With double brooding as rare as it is in the Louisiana Waterthrush, our data are at best suggestive. But of the 16 birds of known age involved in double brooding, 15 (93.8%) were >1 year old (Table 1), so one may reasonably attribute age as a factor in double brooding. But double brooding can not be extended as a characteristic of individual birds. Waterthrushes typically returned in successive years to previously held territories. As previously reported, among 201 territories, 18% of males and 15% of females had returned at least once, and 13% of males and 7% of females returned at least two times to the same stream to breed (Mulvihill et al. 2008). Although a minimum of 10 of 17 individuals involved in double broods were known to have nested on the same streams in previous years (Table 1), not one double brooded more than a single year.

Similarly, we have few data to evaluate the role of food availability as a factor in the frequency of double brooding (Holmes et al. 1992, Rodenhouse and Holmes 1992, Nagy and Holmes 2005a, b); however, it is notable that almost all of the cases of double brooding we report occurred on comparatively high-quality circumneutral streams. Only a single case of double brooding ("Penrod 2008") was recorded on a stream moderately affected by acidification. In companion studies, mayflies (Ephemeroptera), a favored prey of the Louisiana Waterthrush, were almost completely absent from acidified streams and were replaced by several acid-tolerant genera of stoneflies (Plecoptera) (Mulvihill et al. 2008). Further studies should focus on the phenology of insect prey and the potential role of food availability in determining the waterthrush's reproductive strategies. Experimental additions of food may also be made to test mechanistic hypotheses related to food availability. For example, we suggest that early-nesting birds may judge food availability after the fledging of their first brood as an indicator of suitability of conditions for an attempt at a second brood. Such a hypothesis predicts that prey levels at the end of the first nesting attempt are a more important determinant of second nesting attempts than are prey levels at the beginning of the first attempt.

Finally, as we hypothesized, molting is a late-season constraint that may influence the occurrence of double brooding, especially in long-distance migrants (Evan-Ogden and Stutchbury 1996, Ligi and Omland 2007). Molting birds ordinarily become less active and skulk, strategies thought to reduce both demand for energy and the risk of predation (Heise and Rimmer 2000). We have no evidence that pairs that fledged young on or before the mean fledging date ever overlapped molt and breeding. But because fledging dates spanned 8 weeks, while molt onset spanned 5 weeks, it is apparent that after the median fledging date some degree of overlap of molt and breeding was routine. We observed extensive overlap (10–29 days) in four late-nesting pairs whose young fledged after mid-June. Compared to birds that do not begin molt until completing all breeding activity, birds whose molt and breeding overlap likely experience increased energy demand and risk of predation to themselves and their young because they are committed to providing parental care and, therefore, to remaining comparatively active and behaviorally conspicuous while coping with impaired flight abilities resulting from wing molt (Swaddle and Witter 1997, Hedenström 1999, Swaddle et al. 1999).

Notwithstanding molt–breeding overlap, the onset of molt of late-nesting Louisiana Waterthrushes was delayed up to 3 weeks later than the average, a difference similar to that observed between single- and double-brooded Hooded Warblers (*Wilsonia citrina*; Evan-Ogden and Stutchbury 1996). In fall, Louisiana Waterthrushes are among the earliest nearctic–neotropical migrants, regularly arriving even in early August in Panama (Ridgely and Gwynne 1989), Costa Rica (Stiles and Skutch 1989), and the Dominican Republic (Latta, unpubl. data). Provided that their molt and migration do not overlap substantially, double-brooded Louisiana Waterthrushes (and their second-brood young) must be among the latest migrants of their species, perhaps not departing their Pennsylvania breeding grounds before the end of August. In species like the Louisiana Waterthrush that defends winter territories (Eaton 1953, Rappole and Warner 1980, Master et al. 2005, Latta, unpubl. data), late arrivals may be relegated to lower-quality territories or perhaps to non-territorial "floater" status, either of which can have negative consequences on survivorship (Rappole et al. 1989, Winker et al. 1990, Latta and Faaborg 2000, 2001). Furthermore, the Louisiana Waterthrush, which is the sole obligate headwater riparian songbird in its breeding range, must integrate itself into a diverse community of resident stream-adapted songbirds at least on portions of its wintering grounds (Master et al. 2005). If both intra- and/or interspecific competition for a restricted habitat put a high priority on the timely arrival of Louisiana Waterthrushes on their wintering grounds, then our study suggests that there is an important temporal constraint on double brooding (acting through delayed molt) that may be particularly strong in this species. Studies focused on the winter ecology of the species, and the consequences of arrival time and habitat quality, are currently underway.

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