

Timing and duration of egg laying in duetting Buff-breasted Wrens

Sharon A. Gill¹

Department of Biology, York University, 4700 Keele Street, Toronto, Ontario M3J 1P3, Canada

Received 3 October 2001; accepted 25 February 2002

ABSTRACT. Using direct observations of Buff-breasted Wrens (*Thryothorus leucotis*), I examined timing and duration of egg laying, the behavior of females and males around the time of laying, and duetting and solo singing on laying and non-laying mornings. When laying, females roosted either alone in breeding nests or with their mates in dormitory nests, and left them on average 3.5 min before sunrise. Females returned to their nests at 18.6 min after sunrise and took 21.1 min to lay their eggs. Almost all females were accompanied by their mates to the nest before laying, most males foraged near the nest during laying, and nearly all pairs re-united shortly after laying. Pairs sang significantly fewer duets and females gave significantly fewer solo songs on laying versus non-laying mornings, while males did not change their solo singing behavior. Singing was not restricted to times when females were off their nests, as some pairs duetted and some males gave solo songs while females were laying. These results suggest that females lay their eggs at a time of day which is unfavorable in terms of duetting, and, in turn, for defence of mates and territories.

SINOPSIS. Sincronización y duración de la puesta en individuos de *Thryothorus leucotis* que cantan a duo

Mediante observaciones directas en individuos de *Thryothorus leucotis*, examiné la sincronización y la duración de la puesta de huevos, la conducta de ambos sexos al momento de poner, y las canciones a duos o solitarias en mañanas de ovoposición y no puesta. Cuando las hembras van a poner pernoctan solas en su nido reproductivo o con su pareja en nidos contruidos para dormir. Estas abandonan sus dormitorios un promedio de 3.5 minutos previo al amanecer. Las hembras regresan al nido a los 18.6 minutos y toman un periodo de 21.1 minutos en poner. Casi todas las hembras fueron acompañadas por sus parejas al nido, previo a poner. La mayoría de los machos forrajearon en los alrededores del nido durante el tiempo de puesta, y en la gran mayoría de los casos la pareja se unió nuevamente posterior a la puesta. Las parejas vocalizaron significativamente menos a duos o la hembra de forma independiente, en los días de puesta, que en otros días. Por su parte no hubo cambio en la frecuencia de cantos por parte del macho. El canto no estuvo restringido al tiempo en que la hembra estuvo fuera del nido, ya que algunas parejas cantaron a duo o los machos vocalizaron mientras las hembras ponían. Estos resultados sugieren que las hembras ponen a una hora del día que no es favorable en término de vocalizar a duo, y que es más apropiado para la defensa del territorio por parte de la pareja.

Key words: breeding, female behavior, Neotropics, Panama, *Thryothorus leucotis*

The time of day of egg laying and the duration of laying bouts are poorly known for most passerine species. Based on the handful of studies to date, passerines appear to lay either within a restricted period around sunrise or later in the day with significant variation in laying times (e.g., Skutch 1952; Weatherhead et al. 1991; Oppenheimer et al. 1996). Similarly, the time it takes to lay an egg, or laying bout, varies considerably from just a few seconds in several species of brood parasites to over an hour in American Robins (*Turdus migratorius*; Nolan

1978; Muma 1986; Sealy et al. 1995; McMaster et al. 1999; Peer and Sealy 1999). In addition, there is almost no information on the interactions between females and their mates before, during, and after laying. To my knowledge, the only observations that exist were made by Nolan (1978), who reported that male Prairie Warblers (*Dendroica discolor*) rarely escorted females to their nests prior to laying. Other behavioral data, such as singing rates of males (and females in tropical species), and the association of pairs before and after laying, have not been recorded for any passerine species. Precise estimates of laying time and duration, combined with observations of pair interactions around the time of laying, would contribute to our understanding of several aspects of avian

¹ Current address: Department of Ecology and Evolutionary Biology, 569 Dabney Hall, University of Tennessee, Knoxville, Tennessee 37996-1610 USA. Email: sgill1@utk.edu

biology, such as energetics, hatching asynchrony, the timing of brood parasitism and copulations, and patterns of mate guarding (McMaster et al. 1999). Tropical species, in many of which males and females duet and have year-round pairing and territoriality (Farabaugh 1982; Levin 1996a,b; Langmore 1998), are ideal subjects for the study of egg-laying behavior and male and female interactions at laying.

In this paper, I describe the laying behavior of Buff-breasted Wrens (*Thryothorus leucotis*), a Neotropical species in which females sing throughout the year by participating in antiphonal duets with their mates and by producing sex-specific solo songs. A diel peak in duetting and singing occurs around sunrise (S. Gill, unpubl. data), suggesting that females may face a conflict between laying and duetting. The objectives of my study were (1) to determine precise egg-laying times and laying-bout durations in Buff-breasted Wrens by continuous observations of females, (2) to document the behavior of males and females around the time of laying, particularly whether pairs roosted together during the laying period, and whether males accompanied females to their nests and joined them after laying, and (3) to compare rates of duetting and solo singing on laying and non-laying mornings. These are the first observations to examine laying and associated behavior in a tropical, duetting species, and are unique in presenting information on the interactions of pairs around the time of laying.

METHODS

I observed an individually color-marked population of Buff-breasted Wrens from February to July in 1998 and 1999 in a 22-ha secondary forest in Gamboa, Republic of Panamá (9°7'00"N, 79°42'00"W). Buff-breasted Wrens are small (females: 16–19.5 g, males: 18.5–23 g; Gill, unpubl. data) insectivores, which inhabit secondary forests from central Panama to northern and central South America, primarily east of the Andes (Ridgely and Tudor 1989). Males and females pair and maintain territories year-round. Pairs build domed dormitory nests in which they roost overnight, and while eggs are sometimes laid in pre-existing dormitory nests, pairs typically build bulkier nests for breeding.

Beginning in April of both years, I moni-

tored pairs for nest building and checked existing dormitory nests for the presence of eggs. Buff-breasted Wrens lay clutches of two or three eggs; eggs are laid on consecutive days (Gill, unpubl. data). When a nest had one or two eggs, I watched the nest the following morning to record laying of the second or third egg, respectively. As part of a separate study, I watched females and nests that did not have eggs, and in the course of these observations, I fortuitously observed the laying of first eggs as well. I watched nests from a distance of 10 m or more from which I did not noticeably affect the pair's behavior.

I arrived at breeding nests 5–15 min before sunrise and before the wrens had left their nests. I recorded at what time the pair left the nest and in which nest(s) the female and male roosted. After the pair had left their nest(s), I remained within viewing distance of the breeding nest while trying to visually track the birds as they moved around their territory. In cases where it was not possible to do both, I favored watching the nest and tracking the pair by their vocalizations only. I recorded the time that the female re-entered the nest to lay (laying time) and whether the male accompanied the female on her return. Once the female re-entered the nest, I watched it until the female exited, recorded the time, and then followed the female to determine whether the pair reunited. Because breeding nests of Buff-breasted Wrens are domed, I could not observe females while in nests, and therefore could not determine the exact time of oviposition (Nolan 1978). Nests were checked after females left them for the first time in the morning and after the laying bout to confirm the presence of a new egg. All behaviors were recorded to the nearest minute. The duration of the laying bout was calculated by subtracting the time females re-entered the nest to lay from the time they left it after laying. Because each female was observed only once, I did not quantify laying interval or the time between the laying of successive eggs (Schubert and Cooke 1993).

I quantified the number of duets and male and female solo songs given in the morning of a laying bout (hereafter laying morning) as well as the number given on a non-laying morning. Non-laying observations were made in the weeks before females laid their eggs. The breeding season of Buff-breasted Wrens lasts approx-

Table 1. Mean \pm SD time of day of laying and mean \pm SD laying-bout duration (ranges in parentheses) by female Buff-breasted Wrens, according to egg-laying order. The first egg is the first egg laid in the clutch regardless of final clutch size, the penultimate egg is the second egg laid in a three-egg clutch, and the final egg is the last egg laid in a two- or three-egg clutch.

	Laying time relative to sunrise (SR)	Bout duration (min)	<i>N</i>
First egg	SR + 15.8 \pm 7.8 (SR +9 to +26)	17.2 \pm 5.5 (11–25)	5
Penultimate egg	SR + 24.0 \pm 11.3 (SR +17 to +37)	17.3 \pm 0.6 (17–18)	3
Final egg	SR + 17.5 \pm 2.1 (SR +16, +19)	36.5 \pm 2.1 (35, 38)	2
All eggs	SR + 18.6 \pm 8.4 (SR +9 to +37)	21.1 \pm 8.9 (11–38)	10

imately six months (Gill, unpubl. data) and clutch initiation is asynchronous, which made it difficult to standardize the time between laying and non-laying observations (e.g., one week before laying). On average, I made non-laying observations 17.7 days ($N = 10$, range: 8–28 days) before laying occurred. On both laying and non-laying mornings, I quantified the number of duets and the number of male and female solo vocalizations produced in the 30 min following the first duet of the morning. I performed Wilcoxon matched-pairs signed-ranks tests to compare duetting and singing on laying and non-laying mornings.

I present times of day as minutes relative to sunrise, which are represented as SR– or SR+ depending on whether the event occurred before or after sunrise, respectively. Sunrise times for Gamboa were obtained from the United States Naval Observatory Astronomical Applications Department website at aa.usno.navy.mil/AA/. Between the earliest (10 May) and latest (14 June) observations in this study, sunrise time differed by only four minutes; therefore, I did not consider whether sunrise time influenced the laying behavior of females (McMaster et al. 1999). Mean \pm SD sunrise time (Eastern Standard Time) during the study was 0600 \pm 1.4 min.

RESULTS

Over the course of the study, I observed egg laying and associated behavior of 10 females, and compared their behavior on days prior to the initiation of breeding. On non-laying days,

all females roosted with their mates in dormitory nests. On laying days, females roosted alone in breeding nests in five cases, while three females roosted with their mates in dormitory nests. In two cases, I was unable to determine where the female roosted because my initial view of the breeding nest was obscured. Females left their nests on average (\pm SD) 3.5 \pm 6.0 min before sunrise ($N = 6$, range: SR – 10 to SR + 5). In no case had the female laid an egg before leaving the nest for the first time of the day. After leaving their nests, females foraged and duetted with their mates usually within 10 m of breeding nests. Females did not visit their nests between the time when they first left them around dawn and when they returned to lay their eggs.

Females varied slightly in both the time they entered their nests to lay (laying time) and the time it took them to lay (laying-bout duration; Table 1). The mean laying time was SR + 18.6 \pm 8.4 min, and ranged from SR + 9 min to SR + 37 min. The duration of laying bouts ranged from 11 to 38 min for laying of a first and third egg, respectively, with a mean laying bout duration of 21.1 \pm 8.9 min. The shortest laying bout of 11 min occurred when an unidentified female intruded onto the territory and duetted with the male, who had been giving solo songs while his mate was laying. The laying female, who had not responded to her mate's solo songs, immediately left the nest and flew directly to the intruding female, chased her off the territory, and the pair then duetted. The mean \pm SD laying-bout duration with this female excluded was 22.2 \pm 8.7 min. The two

Table 2. Mean \pm SD time of the first duet, and number of duets and male and female solo vocalizations given by Buff-breasted Wrens in the 30 min following sunrise on non-laying and laying mornings. Mean times are given in time relative to sunrise (SR).

	Non-laying	Laying	<i>N</i>	<i>Z</i> ^a	<i>P</i>
First duet	SR - 3.0 \pm 5.8	SR - 5.6 \pm 4.1	10	1.195	0.23
Duets	23.2 \pm 26.1	7.4 \pm 3.0	10	-1.960	0.05
Male solo songs	47.6 \pm 58.2	35.9 \pm 40.4	9	-0.296	0.77
Female solo songs	1.0 \pm 1.0	0.1 \pm 0.3	9	-2.060	0.04

^a Wilcoxon matched-pairs signed-rank test.

longest laying bouts of 35 and 38 min occurred during the laying of the final egg of two- and three-egg clutches, respectively.

Most females were accompanied by their mates when returning to the nest to lay and were joined by their mates immediately or shortly after laying. On nine occasions, males accompanied females when they returned to lay their eggs, while one female returned to her nest alone. Once females were in their nests, their mates perched briefly nearby before they resumed foraging usually within 10 m, and often less than 5 m, of the breeding nest. After leaving their nests following laying, females were immediately joined by their mates ($N = 3$) or they flew directly to them ($N = 2$). Four females were joined 4–11 min after leaving their nests by their mates. In the intervening time, these females foraged silently around their nests. In all cases, pairs immediately duetted once they regained contact with each other. One female flew out of sight once she left her nest, and I was not able to determine when the pair came into contact.

The number of duets and female solo songs given in the first 30 min after sunrise differed between laying and non-laying mornings, while male solo singing did not (Table 2). Pairs gave significantly fewer duets and females gave significantly fewer solo songs on mornings during which they were to lay than on non-laying mornings. In contrast, male solo singing was similar on laying and non-laying mornings. Singing was not restricted to times when females were off their nests prior to or after laying. Rather, while females were laying and out of visual contact with their mate, one pair produced duets, two males gave solo songs, and on three territories, both duetting and male solo singing were given. No females gave solo songs while they were in the nest. The mean time that

the pair gave their first duet of the day did not differ significantly between laying and non-laying mornings (Wilcoxon matched-pairs signed-ranks test, $Z = 1.195$, $P > 0.05$).

DISCUSSION

Buff-breasted Wrens lay within a restricted period of the day, with females entering their nests to lay over a 26-min interval beginning shortly after sunrise. The laying time of Buff-breasted Wrens coincides with the most intense period of duetting and solo singing of the day (Gill, unpubl. data). According to one hypothesis, egg laying should be less likely to occur at such a time because of the potential risk of damage to an oviducal egg or as a result of energy constraints (Schiffnerli 1979; Oppenheimer et al. 1996). However, these factors seem to have a negligible influence on the time of laying in Buff-breasted Wrens as well as other passerine species. Studies on several species have found that laying coincided with peak periods of activity, female activity did not change before and after laying, and aerial foragers, which presumably are at greater risk of damaging their eggs, did not lay first thing in the morning before becoming active (Feare et al. 1982; Weatherhead et al. 1991; Oppenheimer et al. 1996; Skutch 2001; this study). Thus, laying times appear to be determined primarily by physiological mechanisms involved in egg formation, such as hormone surges and ovulation, with the result that laying times per se are not under selection at all (Oppenheimer et al. 1996).

Since laying coincides with peak diel duetting, the duration of laying bouts of female Buff-breasted Wrens may be short to minimize overlap between the two activities. The mean laying-bout duration of females was 21.1 min and ranged from 11 to 38 minutes. Laying-

bout durations of 20 north-temperate passerine species, in which female song is not noted to regularly occur, range from 20.7 min in Orchard Orioles (*Icterus spurius*) to over 90 min in American Robins (Nolan 1978; Muma 1986; Sealy et al. 1995; McMaster et al. 1999). Thus, laying-bout duration in Buff-breasted Wrens falls at the lower end of the spectrum, but it is not considerably shorter than in species where females do not sing. Laying-bout duration in Buff-breasted Wrens does appear much shorter than in its congener, the Carolina Wren (*T. ludovicianus*). Observations are scanty, but those made at one Carolina Wren nest over the entire laying cycle of five days found a mean bout duration of 44.4 min (range: 30–64 min; Nice and Thomas 1948), over twice the mean recorded for Buff-breasted Wrens. While female Carolina Wrens use vocalizations in aggressive interactions with other females, only males take part in peak singing around sunrise (Haggerty and Morton 1995). These findings suggest that laying duration in Carolina Wrens may not be under the same selection pressures as in female Buff-breasted Wrens, and that Buff-breasted Wrens may have shorter laying bouts so as to spend more time duetting with their mates. More data are needed on additional *Thryothorus* species displaying both duetting and male-only singing to test the hypothesis that species in which females duet have shorter laying bouts to reduce overlap with duetting.

Duetting and solo singing rates differed between laying and non-laying mornings. Pairs duetted less frequently on mornings when females were laying than on days prior to breeding. Females gave fewer solo songs when they were laying, whereas males maintained a similar rate of solo singing on laying and non-laying mornings. The decrease in duetting rate between laying and non-laying mornings did not occur simply because females did not vocalize during laying events. Rather, laying did not preclude duetting, as almost half of laying females duetted with their mates, and further, the mates of others gave male solo songs while females were in their nests. Males may continue to sing as part of territorial defence, with females forced to respond to their mates' vocalizations if by not doing so there is an increased likelihood of additional females being attracted to the territory. A female intruder on a territory in which the resident female had not responded

to her mate's singing indicates that such a risk does exist.

Most female Buff-breasted Wrens were accompanied by their mates to the nest before laying, males foraged close to the nest during laying, and pairs were re-united shortly after laying. An obvious interpretation of this behavior is that males are guarding their fertile mates from copulation attempts by extra-pair males. In most cases, copulations in the hour following egg laying actually have a reduced likelihood of fertilizing eggs relative to copulations at other times of the day (Birkhead et al. 1996). However, in species with small clutches, such as Buff-breasted Wrens, males may benefit from copulating with females after they have laid eggs because there are limited opportunities for copulations during the short fertile period (Birkhead et al. 1996). Extra-pair males may seek copulations with females at this time for similar reasons, although few or no extra-pair young have been found in the handful of tropical species with long-term pair bonds studied to date (Stutchbury and Morton 2001). If Buff-breasted Wrens follow this emerging pattern, it is unclear why most males escort their mates before and after laying. Some females sought out their mates after laying as well, suggesting an alternative explanation that both sexes may be guarding their pair bond against divorce (Hall 2000). Buff-breasted Wrens occasionally abandon their mates and territories for positions elsewhere (Gill, unpubl. data), so pair associations around egg laying may function to preempt divorce by either member of the pair.

ACKNOWLEDGMENTS

I am grateful to the Autoridad Nacional del Ambiente for permission to work in Panama and the Smithsonian Tropical Research Institute for excellent logistical support. M. A. Mico made several of the laying observations, and E. C. Edwards, M. A. Mico, and M. J. Vohnhof helped locate and monitor nests. For comments on the manuscript I thank L. S. Johnson, D. G. McMaster, B. J. M. Stutchbury, M. J. Vohnhof, and an anonymous reviewer. This study was supported by grants and scholarships from the American Ornithologists' Union's Herbert and Betty Carnes Fund, the American Museum of Natural History's Frank M. Chapman Memorial Fund, Animal Behavior Society, Ontario Graduate Scholarships, Sigma Xi, York University, the Natural Science and Engineering Research Council of Canada (grant to B. J. M. Stutchbury), and the Smithsonian Institution (grants to E. S. Morton and B. J. M. Stutchbury).

LITERATURE CITED

- BIRKHEAD, T. R., E. J. A. CUNNINGHAM, AND K. M. CHENG. 1996. The insemination window provides a distorted view of sperm competition in birds. *Proceedings of the Royal Society of London Series B* 263: 1187–1192.
- FARABAUGH, S. M. 1982. The ecological and social significance of duetting. In: *Acoustic communication in birds*, vol. 2 (D. E. Kroodsma and E. H. Miller, eds.), pp. 98–124. Academic Press, New York.
- FEARE, C. J., P. L. SPENCER, AND D. A. T. CONSTANTINE. 1982. Time of egg-laying of Starlings *Sturnus vulgaris*. *Ibis* 124: 174–178.
- HAGGERTY, T. M., AND E. S. MORTON. 1995. Carolina Wren (*Thryothorus ludovicianus*). In: *The birds of North America* (A. Poole and F. Gill, eds.), no. 188. Academy of Natural Sciences, Philadelphia, PA and American Ornithologists' Union, Washington, D.C.
- HALL, M. 2000. The function of duetting in magpie-larks: conflict, cooperation, or commitment? *Animal Behaviour* 60: 667–677.
- LANGMORE, N. E. 1998. Functions of duet and solo songs in female birds. *Trends in Ecology and Evolution* 13: 136–140.
- LEVIN, R. N. 1996a. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*. I. Removal experiments. *Animal Behaviour* 52: 1093–1106.
- . 1996b. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*. II. Playback experiments. *Animal Behaviour* 52: 1107–1117.
- MCMASTER, D. G., S. G. SEALY, S. A. GILL, AND D. L. NEUDORF. 1999. Timing of egg laying in Yellow Warblers. *Auk* 116: 236–240.
- MUMA, K. E. 1986. Seasonal changes in the hour of oviposition by Red-winged Blackbirds in south-western Ontario. *Journal of Field Ornithology* 57: 228–229.
- NICE, M. M., AND R. H. THOMAS. 1948. A nesting of the Carolina Wren. *Wilson Bulletin* 60: 139–158.
- NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. *Ornithological Monographs* 26.
- OPPENHEIMER, S. D., M. E. PEREYRA, AND M. L. MORTON. 1996. Egg laying in Dusky Flycatchers and White-crowned Sparrows. *Condor* 98: 428–430.
- PEER, B. D., AND S. G. SEALY. 1999. Laying time of the Bronzed Cowbird. *Wilson Bulletin* 111: 137–139.
- RIDGELY, R. S., AND G. TUDOR. 1989. *The Birds of South America*. University of Texas Press, Austin, TX.
- SCHIFFERLI, L. 1979. Warum legen Singvögel (Passeres) ihre Eier am frühen Morgen? *Ornithologische Beobachter* 76: 33–36.
- SCHUBERT, C. A., AND F. COOKE. 1993. Egg-laying intervals in the Lesser Snow Goose. *Wilson Bulletin* 105: 414–426.
- SEALY, S. G., D. L. NEUDORF, AND D. P. HILL. 1995. Rapid laying by Brown-headed Cowbirds *Molothrus ater* and other parasitic birds. *Ibis* 137: 76–84.
- SKUTCH, A. F. 1952. On the hour of laying and hatching of birds' eggs. *Ibis* 94: 49–61.
- . 2001. Life history of the Riverside Wren. *Journal of Field Ornithology* 72: 1–11.
- STUTCHBURY, B. J. M., AND E. S. MORTON. 2001. *Behavioral ecology of tropical birds*. Academic Press, New York.
- WEATHERHEAD, P. J., R. D. MONTGOMERIE, AND S. B. MCRAE. 1991. Egg-laying times of American Robins. *Auk* 108: 965–967.