

Breeding biology of the White-rumped Swallow (*Tachycineta leucorrhoa*; Hirundinidae) in a wetland: a comparative approach

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ABSTRACT

We studied the reproductive biology of the White-rumped Swallow (*Tachycineta leucorrhoa*) in a colony of 50 nests boxes located in a wetland of the Paraná River, Santa Fe, Argentina between 2004 and 2006. The nest boxes were checked regularly and reproductive parameters, as well as morphological data of eggs and nestlings, were recorded. The species had an average clutch size of 4.7 eggs whose volumes and weight means were 2.04 cm³ and 2.17 g. respectively. The incubation period averaged 15.9 days and decreased with the clutch size. The mean nestling period was 23.8 days. Clutch size, number of nestlings per nest and the nestling period decreased with the advance of the breeding seasons, while the incubation time increased. Breeding parameters showed a similarity with those reported for the population from Chascomús site, although the eggs were 5% heavier, the incubation period took one more day and the reproductive success was also higher. With the closely related species *Tachycineta meyeni*, the studied species showed a lower clutch size. Finally, considering another closely related species *Tachycineta bicolor*, the White-rumped Swallow showed the reproductive life history traits characteristic of species in the southern hemisphere. We provide new information for this species nesting on wetlands, a fact that contributes to the understanding of changes in the life history of the *Tachycineta* genus along the American continent.

Keywords: birds, life history, *Tachycineta* spp., reproductive parameters

1. INTRODUCTION

Variation in life history traits may enhance the understanding of an animal's ecology and phylogeny (Russell *et al.*, 2004). Reproduction is one of the most energy demanding periods of a bird's life cycle where many reproductive parameters (e.g. nestling size, brood size and laying date) may be correlated with these requirements and the environment's capacity to provide enough resources to satisfy them (Ricklefs, 1974; Drent and Daan, 1980; Clutton-Brock, 1991). However, these same traits may be affected by selection pressures that could lead to new adaptive patterns (Stearns, 1992). Since intraspecific variation is understood as being due to environmental effects, and variation among species is recognised as the adaptive outcome of different selection pressures (McCarty, 2001), it is important to compare local results at these different levels.

Intraspecific variation of reproductive parameters across species' distribution ranges have been widely studied. For instance, in the northern hemisphere, the

positive relationship between clutch size and latitude (Klomp, 1970; Kulesza, 1990; Dunn *et al.*, 2000) and the decline in clutch size with the advance of the breeding season (Murphy, 1986; Stutchbury and Robertson, 1988; Perrins and McCleery, 1989; Winkler and Allen, 1996) has been detected in several species.

At an interspecific level, the life histories of birds in temperate regions of the southern hemisphere resemble more closely those of the tropical regions (Martin *et al.*, 2000; Russell *et al.*, 2004). They have smaller clutch sizes, larger eggs masses, lower adult mortalities, slower developmental rates and shorter parental care than birds of the temperate areas of the northern hemisphere (see review in Martin, 2004).

However, proposed explanations for the generalisations about life history variations have been controversial topics among scientists (e.g. Lack, 1948, 1954, 1968; Stearns, 1976; Zach, 1982; Houston *et al.*, 1983; Weidinger, 1996; Nooker *et al.*, 2005). These patterns mostly rely on data from species in the northern hemisphere and only from a few species in

the southern hemisphere (Moreau, 1944; Yom-Tov *et al.*, 1994; Young, 1994; Martin, 2004). This makes comparisons difficult (Martin, 1996; Mezquida, 2002; Massoni *et al.*, 2007) and evidences the need for information for species from the southern hemisphere.

The genus *Tachycineta* (Hirundinidae) includes nine species endemic to the Americas, ranging from Alaska to Tierra del Fuego (Turner and Rose, 1989). There are three species present in Argentina with the White-rumped Swallow (*Tachycineta leucorrhoa*) being the most studied (see Massoni *et al.*, 2007). Detailed data on its reproductive biology has been provided for Buenos Aires Province (Massoni *et al.*, 2007); while for Santa Fe Province (510 km away from Buenos Aires) the only data available are from de la Peña (2010) who provides information from 15 nests (in 34 years) with eggs or chicks.

The aim of this study was to obtain data on the reproductive parameters of the White-rumped Swallow nesting in nest boxes at wetlands in the Paraná River floodplain (east-central Argentina). We addressed the temporal and spatial scale variations of reproductive parameters, allowing us to make both intraspecific comparisons with the population of *T. leucorrhoa* at Chascomús, Buenos Aires (Massoni *et al.*, 2007), and interspecific comparisons with data for the Chilean Swallow (*Tachycineta meyeni*; Liljeström *et al.*, 2009) and the Tree Swallow (*Tachycineta bicolor*; e.g. McCarty, 2001). Given that the size ranges of these three species all lie between 12 and 15 cm, it was considered that comparisons would not be affected by allometric differences (Robertson *et al.*, 1992; Narosky and Yzurieta, 2003).

2. MATERIALS AND METHODS

We studied pairs of *Tachycineta leucorrhoa* breeding in nestboxes in a wetland on the floodplain of the Colastine River, in the middle section of the Paraná River, Santa Fe Province, Argentina (31°39'40"S–60°35'33"W). The study site is a partially flooded area that belongs to the Ecoregion Delta and Paraná islands (Burkart, 1999). The climate is humid-subtropical mesothermal, with average annual temperature of 18°C (Panigatti *et al.*, 1981). Mean annual temperature during the three studied years (2004–2006) was 19.7°C, and the monthly mean daily temperatures and rainfalls during the breeding seasons ranged from 12.6°C and 15.6 mm in September to 25.6°C and 357 mm in December.

Sixty wooden nest-boxes were placed on wooden poles 1.6 m above the ground that were separated by at least 20 m. The external sizes of the boxes were

25.4 × 16.5 × 17.8 cm (height, width, depth), while the internal ones were 23.8 × 12.7 × 12.7 cm. Boxes had a 3.5 cm diameter entrance hole and a lateral opening that allowed us to monitor the nesting progress of the nest.

Systematic monitoring of the boxes began in late August. Nest boxes were visited on alternate days during nest building and daily during laying. Nests were monitored every two days during incubation except near the expected hatching date, when we checked nests daily. Nests were also visited in the days corresponding to the measurement of the chicks, and every day were checked carefully during the presumed date of fledging.

We considered 30 August as the first day of the breeding season (all dates are reported relative to that day; i.e. number of days from 30 August) and the date of the first laid egg as the starting date of each nest. We determined the length of the breeding season for each year by dating the initiation of the first and last clutch of the season.

Eggs were marked with waterproof ink, measured (length and width) to the nearest 0.01 mm using plastic caliper and weighed to the nearest 0.1 g with a Pesola spring scale. The egg volume was calculated as $\text{length} \times \text{width}^2 \times 0.507$ (Manning, 1979) and clutch volume was calculated as the sum of the volume of all eggs laid in a clutch. Final clutch size was recorded when no additional eggs were laid for two consecutive days. We considered the hatching date (day 0) to be the date on which the majority of eggs in the clutch hatched.

The incubation time was calculated as the time elapsed since the penultimate egg was laid until first egg hatched. The onset of incubation was measured this way from previous observations of asynchronous hatching chicks, where $n - 1$ eggs hatched on the same day and the remaining one on the next day.

The nestling period was estimated as the number of days elapsed since the first egg hatched until all nestlings left the nest. Chicks were weighed to the nearest 0.1 g with a Pesola spring scale on days 3, 6, 9 and 12 of age. Chicks were not measured after day 12 to prevent premature fledging. Accordingly, it was not possible to determine the asymptotic weight directly from the measurements, so we fitted the data to a logistic growth equation, relating body mass to age using a least squares method, as proposed by Ricklefs (1967):

$$Y(t) = A/[1 + e(-K(\text{age} - t_i))],$$

where: $Y(t)$ = body mass (g) of the chick at age t (days), A = asymptotic body mass (g), K = growth constant (1/day), t_i = inflection point of the growth curve (days). We calculated the inverse measure of growth

rate, that is, the time required to grow from 10 to 90% of the asymptote, using the formula $4.4/K$.

We analysed the relationship between several parameters prior to hatching: initial clutch size (number of eggs at the end of laying), final clutch size, egg survival (ratio between the final and initial clutch size). Post-hatching, the parameters recorded were: number of hatched chicks, hatching success (ratio between number of hatched chicks and final clutch size), number of chicks present in the previous days to fledging (fledglings), fledging success (the proportion of nestlings in the nest that fledged). Overall nesting success was the ratio between the number of fledglings that fledged and the eggs laid, and nest survival was the proportion of nests initiated that fledged at least one chick.

Tests of normality (Kolmogorov–Smirnov's test, residues analyses) and homoscedasticity (Levene) were conducted to determine whether to use parametric statistical tests. A total of 64 nests were monitored but the number of nests used in different analysis varied depending on the data collected for each nest. As the eggs and nestlings belonging to the same clutch are not statistically independent (*i.e.* they are incubated and reared by the same adults or compete for food resources) their measurements were averaged by nest and used to obtain populations values. Females were not banded and second broods were not identified, so we separated the first and second half of the breeding season to reduce its effect. We used correlation coefficients and regressions to analyse the effect of the egg laying date. Reported values are means \pm standard deviation, and we included the median (*M*) for non-normally distributed variables. All tests were two tailed, and differences were considered significant at $P < 0.05$. We analysed data using STATISTICA 8.0.

3. RESULTS

3.1 Nest box occupation and length of the breeding season

Nest box occupation was 16% ($n = 8/50$ nests) in 2004, 47% ($n = 23/49$ nests) in 2005 and 65% ($n = 33/51$ nests) in 2006. The breeding season

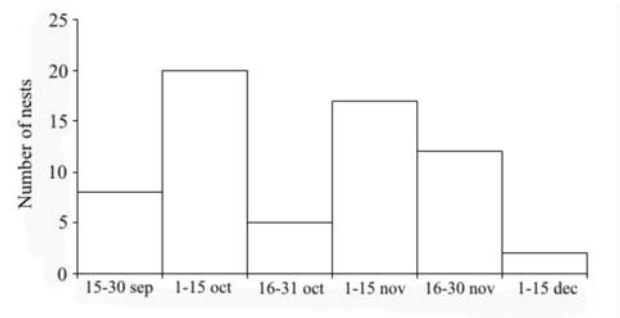


Figure 1 The number initiated nests per half month of the White-rumped Swallow during the breeding seasons of 2004, 2005 and 2006, Santa Fe, Argentina.

lasted approximately 99 days, where most nesting attempts were registered in early October (earliest: 26 September, last: 5 December, Figure 1). The laying date of the first clutches significantly differed among years (Kruskal-Wallis test = 7.21; d.f. = 2; $P = 0.027$): 2004: $72.13 (\pm 20)$ days; 2005: $63.75 (\pm 20.8)$ days and 2006: $49.82 (\pm 23)$ days).

3.2 Egg stage

Clutch sizes ranged from four to six eggs; 21, 41 and two nests had four, five and six eggs, respectively, averaging 4.70 ± 0.52 eggs ($M = 5$, $n = 64$ nests). The pure white eggs from 64 clutches averaged $20.25 (\pm 0.99) \times 14.13 (\pm 0.56)$ mm (length \times width), and weighed $2.17 (\pm 0.21)$ g. Mean egg volume was $2.04 (\pm 0.14)$ cm³ ($n = 64$ clutches) and average clutch volume was $9.66 (\pm 1.51)$ cm³ ($n = 49$ clutches). Egg survival was $0.91 (\pm 0.27)$; $M = 1$, $n = 63$ clutches).

Incubation lasted on average 16 days and varied between clutch sizes (Table 1). There was a negative correlation between clutch size and incubation time (Spearman $r = -0.37$, $n = 57$ clutches, $P = 0.005$).

Hatching success was $0.88 (\pm 0.19)$; $M = 1$; $n = 59$ nests) and did not differ between clutches of four (0.84 ± 0.26 ; $M = 1$; $n = 17$) and five (0.86 ± 0.21 ; $M = 1$; $n = 39$) eggs (Mann–Whitney test; $U = 300$, $P = 0.5$).

Table 1 Variation in mean (\pm SD) incubation times of the White-rumped Swallow with different clutch sizes

Clutch size (eggs)	Incubation time (days)	Median	Nests
All sizes pooled	15.88 (± 0.96)	16	58
Four	16.31 (± 0.79)	16	16
Five	15.77 (± 0.96)	16	39
Six	14.5 (± 0.71)	15	3

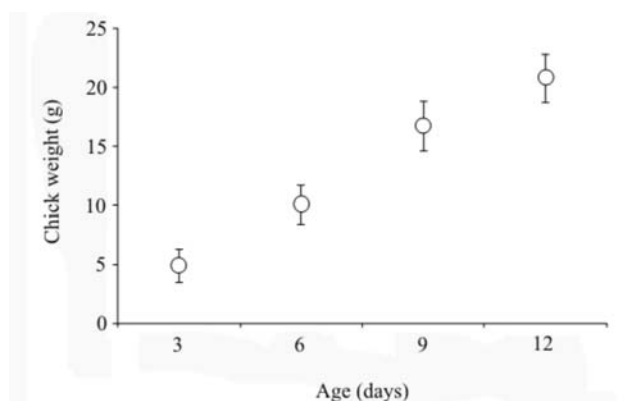


Figure 2 Mean (\pm SD) chick weight (g) by brood as a function of age (days) for the 2004, 2005 and 2006 breeding seasons, Santa Fe, Argentina. The numbers of broods were 43, 43, 37 and 32 for the days 3, 6, 9 and 12, respectively.

3.3 The nestling stage

The number of nestlings in a brood averaged 3.8 (± 1.5 ; $M=4$, $n=63$ nests). The nestling period lasted 17–29 days with a mean of 23.8 (± 3.0) days ($M=23$; $n=51$ nests). The nestling period slightly increased with the numbers of nestling hatched but only approached significance (Spearman $\rho = 0.25$; $P = 0.08$; $n = 51$ nests), and did not vary with the number of nestlings that fledged (Spearman $\rho = 0.19$; $P = 0.19$; $n = 51$ nests).

Nestlings weighed 4.94 g (± 1.39 ; $n = 43$ brood average) at day three reaching 20.82 g (± 2.02 ; $n = 32$ brood average) at day 12 (Figure 2). Estimated asymptotic weight was 22.9 g. Once fledged, the chicks did not return to the nest. Fitting the weight as a function of chick's age to a logistic growth curve showed a constant growth rate, K , of 0.399 g/day. Brood reduction occurred in 10 nests resulting in the death of 1.7 ± 0.7 nestlings per nest. Fledgling success was determined in 51 nests where at least one chick fledged, and averaged 0.92 ± 0.18 ($M=1$). Nesting success was 0.65 ± 0.38 ($M=0.78$; $n = 64$ nests).

3.4 Nest failures

Nest survival averaged 0.8 ($n = 64$ nests) and varied from 0.96 in 2005 ($n = 23$ nests) to 0.76 in 2006 ($n = 33$), although this difference was only slightly significant (Fisher exact test, $P = 0.067$). In 2004 averaged 0.5 ($n = 8$), but it was excluded from comparisons because of its small sample size.

A total of 13 nests (20%) did not produce any fledgling. During the egg stage, the swallows lost six (46%) breeding attempts, with complete disappearance of the eggs or the presence of broken egg shells inside the nest. During the nestling stage, the swal-

lows lost seven (54%) breeding attempts, with the presence of dead nestlings inside the nest or no nestlings. A total of 14 nests (22%) experienced brood reduction either during the egg stage ($n = 4$) or the nestling stage ($n = 10$). Even though the information about the causes is scarce, we detected a sudden drop in air temperature for the couple of days leading up to the time when dead nestlings were observed in some nests. Mortality may have been due to starvation because this species is an aerial insectivore. In addition, during nest checks, we found some adults of the Patagonia green racer (*Philodryas patagoniensis*) inside the nest boxes. During our next visit to these nests, eggs and chicks that had been present had disappeared.

3.5 Relationship of variables with time of the breeding season

Clutch size (total, first and second half), clutch volume (total and first half) and nestlings hatched per brood significantly decreased with the advance of the breeding season. On the other hand, incubation period and weight of chicks at day 6 of age increased. Other variables remained constant throughout the breeding season (Table 2).

4. DISCUSSION

Data obtained for *T. leucorhoa* at the Santa Fe site were generally comparable to the conspecific populations studied in Chascomús (Buenos Aires, Argentina) by Massoni *et al.* (2007); (e.g. timing and extent of the breeding seasons, clutch size, egg size and nestling period). However, there were differences in egg mass (5% heavier in Santa Fe), incubation period (approximately 1 day longer in Santa Fe) and reproductive success and associated variables (brood reduction, egg and nest survival).

In most bird species, individuals that lay later in the breeding season tend to lay fewer eggs per clutch than those that lay earlier (e.g. Hochachka, 1990; but see Young, 1994). This pattern of clutch size reduction with the progress of the breeding season was also found in this study, in agreement with that reported for this species in Chascomús. This same reduction was found when we analysed separately the first and second half of the breeding season. Egg size, however, did not vary with the progress of the breeding season, in contrast to the reduction found by Massoni *et al.* (2007).

Incubation is a period of high demand of energy and time from adults, equivalent to the stage of the nestlings (Williams, 1996; Tinbergen and Williams, 2002). The positive correlation found between incu-

Table 2 Relationship of reproductive parameters of the White-rumped Swallow with time of the breeding season

Variable	Test	Type	Nests	P
Clutch size	Spearman, $\rho = -0.65$	–	64	<0.01
Clutch size (1st half)	Spearman, $\rho = -0.39$	–	33	0.025
Clutch size (2nd half)	Spearman, $\rho = -0.5$	–	31	0.004
Egg length, width, weight and volume	Linear regression, $R^2 \leq 0.037$	NV	57	≥ 0.15
Clutch volume total	Linear regression, $R^2 = 0.14$	–	49	<0.01
Clutch volume 1st half	Linear regression, $R^2 = 0.31$	–	29	<0.01
Clutch volume 2nd half	Linear regression, $R^2 = 0.01$	NV	20	0.64
Egg survival	Spearman, $\rho = -0.02$	NV	64	0.9
Incubation period	Spearman, $\rho = 0.34$	+	58	<0.01
Hatching success	Spearman, $\rho = -0.09$	–	59	0.49
Nestlings hatched per brood	Spearman, $\rho = -0.38$	–	63	<0.01
Fledging success	Spearman, $\rho = 0.02$	NV	57	0.91
Nestling period	Spearman, $\rho = -0.26$	–	51	0.067
Weight of chicks from day 3	Spearman, $\rho = 0.02$	NV	43	0.9
Weight of chicks from day 6	Spearman, $\rho = 0.5$	+	43	0.001
Weight of chicks from day 9	Spearman, $\rho = -0.26$	NV	37	0.1
Weight of chicks from day 12	Spearman, $\rho = -0.07$	NV	32	0.7

+ Positive relationship; – negative relationship; NV, no variation.

bation period and the advance of the breeding season agrees with the fact that the optimal conditions should be present early in the season (Lack, 1968). Under this scenario, food resources would be more abundant and, as a consequence, incubation periods would be shorter and clutches larger. This is consistent with the negative correlation found in our study (but not in Chascomús) between incubation period and clutch size.

There was higher egg survival in Santa Fe, nest survival and nesting success was also higher than at Chascomús (0.54 and 0.49 respectively), in spite of a higher brood reduction during the nestling period (28%). When comparing failures between egg and nestling stages, they were very similar Santa Fe while in Chascomús they mostly occurred during the egg stage.

Differences found between Santa Fe and Chascomús' populations would be an outcome of intraspecific variation associated with environmental conditions (Brawn, 1991; Badyaev and Ghalambor, 2001), especially if we consider that, despite of

similarities in reproductive parameters, the reproductive success was markedly different.

Regarding interspecific comparisons, clutch size did not increase with latitude when compared to *T. meyeri* (Ushuaia, Argentina) but incubation period and time of parental care did (Liljeström *et al.*, 2009). Finally, with respect to its northern hemisphere congener *T. bicolor* (mainly in Canada and Norwest from the USA), the White-rumped Swallow showed the life history traits characteristic of southern hemisphere species relative to their northern hemisphere counterparts. Its species exhibited a lower clutch size, approximately one egg less (Zach, 1982; Butler, 1988; Ramstack *et al.*, 1998; Murphy *et al.*, 2000), eggs greater in length (7%), width (7%), volume (19.5%) (Robertson *et al.*, 1992) and an egg weight 15% heavier (Ramstack *et al.*, 1998; Whittingham and Dunn, 2001). *T. leucorroha* also showed a 25% lower growth rate (McCarty, 2001), an incubation period of about 1 day longer than *T. bicolor* (Robertson *et al.*, 1992), and accordingly a more extended parental care (3 days longer–McCarty,

Table 3 Comparative table of reproductive parameters (mean values) between the White-rumped Swallow, the Tree Swallow and the Chilean Swallow

Variable	<i>T. bicolor</i> (USA-Canada)	<i>T. meyeri</i> (Ushuaia-AR)	<i>T. leucorroha</i> (Chascomús-AR)	<i>T. leucorroha</i> (Santa Fe-AR)
Clutch size (eggs)	5.6 ^a	4 ^f (modal)	4.92 ^e	4.70
Egg length (mm)	18.5 ^b	–	20.01 ^e	20.25
Egg width (mm)	13.2 ^b	–	14.04 ^e	14.13
Egg volume (cm ³)	1.65 ^b	–	2.05 ^e	2.04
Egg weight (g)	1.84 ^c	–	2.06 ^e	2.17
Growth rate (g/day)	0.49–0.56 ^d	–	0.46 ^e	0.399
Incubation period (days)	14.5 ^b	17.5 ^f	14.8 ^e	15.88
Parental care (days)	21 ^d	26.5 ^f (modal)	23.3 ^e	23.8

Data extracted from: ^aMurphy *et al.* (2000); ^bRobertson *et al.* (1992); ^cRamstack *et al.* (1998); ^dMcCarty (2001); ^eMassoni *et al.* (2007); ^fLiljeström *et al.* (2009).

2001. Table 3). These differences are consistent with those reported for the species in Chascomús site, except for the incubation period in which no difference was found.

In conclusion, as well as expanding our knowledge of the reproductive biology of the White-rumped Swallow for the study area, we have provided new information for this species nesting on wetlands in the floodplain of the Paraná river; a fact that contributes to the understanding of changes in life history of this genus along the American continent. Thus, we have provided evidence about the suspected dissimilarities between the life history traits of birds between the southern and northern hemispheres. This is particularly relevant if we consider that these differences are not clear due to the limited knowledge of the South American birds' life history traits (Martin, 1996; Mezquida, 2002).

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