Ibis (2007), **149**, 10–17

Breeding biology of the White-rumped Swallow *Tachycineta leucorrhoa* in Buenos Aires Province, Argentina

VIVIANA MASSONI*, FLORENCIA BULIT & JUAN CARLOS REBOREDA
Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Intendente Güiraldes 2160, C1428EGA – Capital Federal, Argentina

We conducted a study of the breeding biology of the White-rumped Swallow *Tachycineta leucorrhoa* nesting in nestboxes in a flat, farming landscape in Buenos Aires Province, Argentina. White-rumped Swallow nesting attempts were detected from the end of September to mid December, with most clutches laid during October. Birds laid clutches of 4–6 eggs with a mode of five eggs; most broods hatched synchronously (58%), but hatching spread could last up to 4 days. Nestling growth curves adjust well to logistic functions, and at day 15 nestlings attain the asymptotic weight of 21.6 g. Clutch size in White-rumped Swallows declined significantly as the season progressed. In addition, late-season eggs were smaller and late-season nestlings had a shorter nestling period and lower weight at day 15, probably leaving the nest lighter than early-season nestlings. These data suggest that the Swallows would benefit greatly from laying early in the season, which would provide nestlings with better survival prospects. However, both major sources of nest mortality, interspecific competition for nest-sites and nestling mortality during bad weather, decreased through the season. White-rumped Swallows follow the pattern found for other southern species, as it has smaller clutch size, lower growth rate and remains longer at the nest than its Northern Hemisphere congener the Tree Swallow *Tachycineta bicolor*.

Current perspectives and tests on avian life history are mainly based on northern temperate systems, which include fewer than 25% of the bird species worldwide (Martin 2004). Simultaneously, there is increasing comparative evidence that the patterns of avian life-history variation in southern temperate regions are more similar to those of tropical birds than to northern temperate populations (Martin 1996, Martin *et al.* 2000, Russell *et al.* 2004). Tropical and southern populations have smaller clutch sizes, higher egg mass, lower adult mortality, slower developmental rates and long parental care duration (Martin 2004 and references therein). It has been argued that the relatively stable environments of the tropics and the Southern Hemisphere with the lack of a severe winter, and a high proportion of nest predators in these regions, are responsible for these differences in life-history parameters (Ashmole 1963, Skutch 1985, Martin *et al.* 2000).

In a similar way, the decline in clutch size as the breeding season progresses is well documented in northern temperate regions (Murphy 1986, Stutchbury & Robertson 1988, Perrins & McCleery 1989, Hochachka 1990, Winkler & Allen 1996; for exceptions see Crick *et al.* 1993), but information on the occurrence of such declines and its characteristics, or its absence (Moreno *et al.* 2005), is scant for the Southern Hemisphere. With the exception of studies focusing on the variation of clutch size and its proximal and ultimate causation, there is a dearth of information on Southern Hemisphere species life-history traits such as egg mass, hatching asynchrony, developmental rate, parental effort and age of first reproduction.

The genus *Tachycineta* includes nine swallow species endemic to the Americas, ranging from Alaska to Tierra del Fuego (Turner & Rose 1989). The most extensively studied is the Tree Swallow *Tachycineta bicolor*, and its use as a model organism has provided valuable insight into many topics of avian biology and life-history traits (Jones 2003). Although information on other congeners has been gathered (Dyrcz 1984,

---

*Corresponding author.
Email: massoni@ege.fcen.uba.ar

Allen 1996, Moore *et al.* 1999), many of them remain poorly known. Available information on the breeding biology of the White-rumped Swallow *Tachycineta leucorrhoa* is, at best, scant. This is a temperate species whose distribution ranges from southern Brazil, Paraguay, Uruguay and northern Argentina (south to La Pampa and Buenos Aires) (Ridgely & Tudor 1989). In Buenos Aires Province, Sclater and Hudson (1889) described its clutch size as ranging from five to seven eggs, Pereyra (1969) found up to five eggs in their nests (number of nests recorded unknown), and Mason (1985) characterized ten nests, four during the egg stage, with a clutch size of 4–6 eggs and a mean value of 4.75. Finally, De la Peña (1996) found 16 nests of the species, five in the egg stage, with a mean clutch size of 4.4 eggs at Santa Fe Province, Argentina.

The aim of the present study was to obtain information on the breeding biology of White-rumped Swallows nesting in nestboxes, and to describe their egg morphology and clutch size, egg survival, incubation period, hatching and fledgling success, growth of nestlings, etc., to evaluate how they change, if at all, as the season progresses, and to report such information in a way that allows for comparison with the extensively known Tree Swallow.

METHODS

We conducted a nestbox study on White-rumped Swallows in a flat, farming landscape at the Instituto Tecnológico de Chascomús, CONICET, beside Chascomús lagoon, Buenos Aires Province, Argentina (35°34′S, 58°01′W), between September and January from 2002 to 2005. In the study area the monthly mean daily temperatures ranged from 12 °C in September to 22 °C in January. The nestboxes were placed 1.3–1.7 m above the ground on fence posts delimiting paddocks, approximately 30 m from each other, distributed in an area of 63 ha. The boxes measured 25 × 17 × 13 cm, had an entrance hole 4 cm in diameter, a lateral door that allowed monitoring of the nest's progress, and a 'wigwag' trap to capture the breeding adults when they enter the box. The trap is activated by pulling a long piece of monofilament fishing line that is attached to a swivelling piece of wood when the bird required enters the box during the trapping period.

Systematic checking of the boxes began in September. Boxes were visited every other day (2002/03 to 2003/04) and daily (2004/05) to detect the start of egg-laying. Eggs were marked with water-proof ink at the lesser pole (foot *sensu* Gosler *et al.* 2005), measured (length and width) to the nearest 0.01 mm using a digital calliper, and weighed to the nearest 0.01 g with an electronic balance (only in 2004/05). As the eggs belonging to the same clutch are not statistically independent from each other, we first averaged measures of the clutch and used those averages to obtain population values. Nests were visited every other day during incubation and daily during the early morning hours on the presumed date of egg hatching (2004/05, every other day in 2002/03–2003/04). Egg volume was calculated as length × width^2 × 0.507 (Manning 1979). Clutch volume was calculated as the sum of the volume of all eggs laid in a clutch.

Chicks were marked on the legs with indelible markers and weighed every 4 days in 2002/03 and 2003/04 and on days 0, 4, 9, 12 and 15 in 2004/05, using spring balances of 10 g with a 0.1-g accuracy for younger nestlings and of 30 g with a 0.2-g accuracy for older nestlings and adults. We captured, measured (head plus bill, flattened wing and weight) and attached numbered aluminium rings to 61 adult females. Captured birds were dyed with a unique pattern of indelible markers on the breast, abdomen and rump, to recognize them from a distance (2003/04 and 2004/05 only). All nestlings were ringed on days 8–10 of life.

We determined the length of the breeding season for each year by dating the initiation of the first and last clutch of the season. We analysed separately first and second clutches laid by identified females, and the relationship between several variables with date of egg-laying. In order to make use of the best available data, we excluded several nests from some analyses as detailed below, and therefore the number of nests used may differ between variables.

Final clutch size was recorded when no additional eggs were laid for two consecutive days. We excluded from the analysis all the nests in which we detected interference from other species during the laying period. We considered the hatching date to be the date on which the majority of eggs in the clutch hatched; synchronous hatching was considered to be when all eggs hatched on the same day. Hatching asynchrony was determined only in 2004/05 clutches because nests were checked daily in that year. The incubation duration was calculated as the time elapsed from the onset of incubation, detected by daily early morning visits, until the first egg hatched. As in the previous case, data reported belong to the 2004/05 breeding season.

The nestling period was estimated as the number of days elapsed since the hatching of the first egg until all nestlings left the nest. A chick's daily mass gain and growth rate was calculated following Ricklefs (1967). To prevent premature fledging, nestlings were not weighed after day 15. Inspection of the growth curve revealed that White-rumped Swallow chicks reached their asymptotic weight at that age or before, as occurs with Tree Swallow nestlings (Zach & Mayoh 1982, Quinney *et al.* 1986). We cautiously checked the nestbox every day to detect the date and number of fledglings. To calculate nest survival (number of nests that produced at least one chick) we excluded any nests whose failure was attributable to human interference. During the study period 22 nests were abandoned after we captured the females. As some of these desertion events occurred during poor weather conditions following capture, human disturbance may not be the only cause of nest desertion.

Statistical analysis

Data were, unless otherwise stated, not normally distributed and non-parametric statistics were applied. When patterns were consistent across years we pooled data to increase sample sizes. We used Spearman's rank correlations and logistic regressions to analyse the effect of egg laying date. Reported values are means ± se, 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 version 5.0 (Statsoft Inc.).

RESULTS

Nestbox occupation and length of the breeding season

We monitored 128 nesting attempts during the 3-year period. The number of available boxes was augmented from 53 in 2002/03 to 66 in 2003/04, and 96 in 2004/05; percentage occupation by White-rumped Swallows during those years was 38, 50 and 78%, respectively. White-rumped Swallows are partially migratory and left our nestbox breeding site during January. Some individuals, however, remained all winter in Buenos Aires Province (Sclater & Hudson 1889; Pereyra 1969), and used nestboxes to roost together (V.M. pers. obs.). They began to defend nestboxes in early August, although egg-laying did not start until the end of September. Nest building activity was first seen during the last week of August; nest composition and construction were as described elsewhere (Bulit & Massoni 2004).

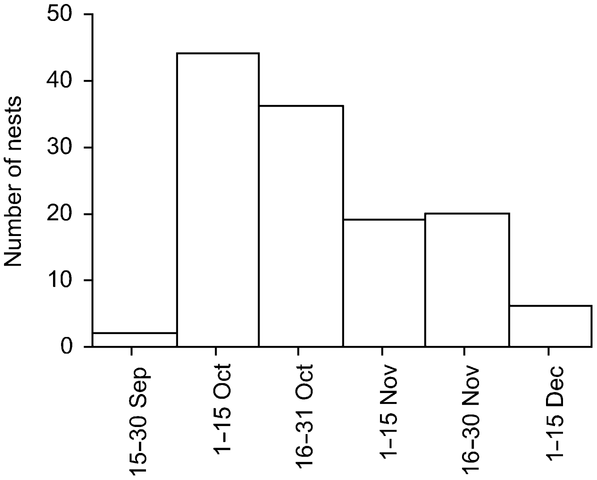

Figure 1. The number of White-rumped Swallow nests initiated per half month ($n = 128$ nests from the 2002/03 to 2004/05 breeding seasons).

The breeding season lasted approximately 3.5 months; the earliest breeding attempt was registered on 29 September and the last one on 12 December, with most clutches laid in October (Fig. 1). There was no difference in egg-laying date of first clutches among years (Kruskal–Wallis test = 0.002, *df* = 2, *P* = 1).

We captured 61 females at their nests during incubation; the morphometric variables were normally distributed, with the female's average head plus bill length 29.5 ± 1.0 mm (27.8–32.0 mm), flattened wing length 116.0 ± 1.0 mm (105.0–126.0 mm) and body weight 22.0 ± 0.2 g (18.8–25 g).

The egg stage

The size of first clutches ranged from four to six eggs (17, 80 and nine nests had four, five and six eggs, respectively), averaging 4.92 ± 0.05 eggs ($M = 5$, $n = 106$ nests). We found a tendency, albeit not statistically significant, to reduce the number of eggs laid in second clutches (4.79 ± 0.15 eggs, $M = 5$, $n = 14$; Wilcoxon matched-pair test = 1.82, $P = 0.07$). Replacement clutches were laid 11.5 ± 1.4 days after failure of the first clutch ($n = 7$). We also recorded four second broods in 2004/05, which were initiated 11 days after successfully raising the first brood (5% of nesting attempts of that year).

The eggs were pinkish-white when first laid and gradually became pure white. Egg measurements did not differ significantly between first and second clutches, so information is reported for both clutches combined. The eggs measured on average 20.01 ± 0.08 × 14.03 ± 0.04 mm (length × width, $n = 118$ clutches) and weighed 2.06 ± 0.02 g ($n = 73$ clutches). The average egg volume was 2.05 ± 0.16 cm^3, and the average clutch volume 9.6 ± 0.15 cm^3 ($n = 118$). Egg mass relative to female body weight was 0.093.

Egg survival was 0.78 ± 0.04 ($M = 1$, $n = 100$) for first clutches, and did not differ between first and second clutches (Wilcoxon matched-pair test = 0.40, $P = 0.69$, $n = 11$). Seven of these breeding attempts involved replacement clutches, and four were true second broods. Incubation lasted 14.8 ± 0.2 days ($M = 15$, $n = 82$), the average increasing from 14.6 days in four-egg clutches to 16.1 days in six-egg clutches (Spearman $r = 0.23$, $n = 82$ clutches, $P = 0.03$).

The nestling stage

Hatching success, the proportion of eggs present in the nest at the end of incubation that hatched, was 0.84 ± 0.03 ($M = 1$, $n = 80$ nests), and did not differ between clutches of four and five eggs (Mann–Whitney *U*-test = 29.5, $P = 0.39$). Hatching spread, determined for 47 clutches during 2004/05, lasted between 1 and 4 days. Nestlings hatched synchronously (within 24 h) in 58% of the nests. The majority of asynchronous nests hatched within 48 h (78%, $n = 14$), 17% within 72 h ($n = 3$) and only one nest within 96 h (5%). In asynchronous nests, 66% of the eggs hatched on the first day. The hatching pattern (synchronous or asynchronous) did not vary between the most common clutch sizes of four and five eggs (Fisher exact test, $P = 0.50$).

The number of nestlings in a brood averaged 4 ± 0.14 ($M = 4$, $n = 69$ nests); their weight at hatching was 1.98 ± 0.04 g ($n = 41$ brood averages), and they reached a peak mass of approximately 22 g around day 15 of life (Fig. 2). Brood reduction occurred in 11 nests and usually followed poor weather conditions, causing the death of 1.7 ± 0.27 nestlings per nest.

The nestling period lasted 21–27 days and averaged 23.3 ± 0.2 days ($M = 23$, $n = 44$). 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 gave a growth rate constant, K, of 0.458 with an asymptotic mass of 21.6 g.

As expected, the nestling period increased with the number of nestlings hatched (Spearman $r = 0.51$, $n = 44$, $P < 0.001$) and fledged (Spearman $r = 0.38$, $n = 44$, $P = 0.01$). Fledgling success, the proportion of nestlings in the nest that fledged, was determined in 69 nests where at least one chick fledged, and averaged 0.95 ± 0.02 ($M = 1$). The number of fledglings per number of eggs laid was 0.49 ± 0.04 ($M = 0.60$).

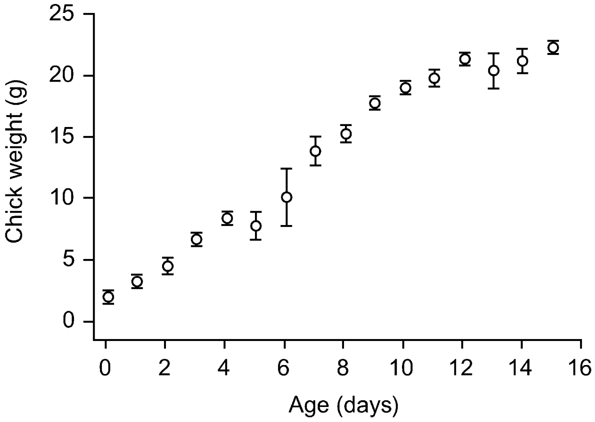

Figure 2. Brood averages of chick weight (g) as a function of age (days) for the 2004/05 breeding season. Dots indicate means ± se. Day 0 corresponds to the hatching day. The number of broods weighed between days 0 and 15 were 41, 11, 6, 13, 42, 3, 2, 4, 18, 42, 5, 16, 40, 4, 14 and 41, respectively.

Nest failures

Nest survival, the proportion of nests initiated that fledged at least one chick, did not differ between years, and averaged 0.54 ± 0.04 ($M = 1$, $n = 128$ nests). During the egg stages the Swallows lost 29 breeding attempts. Sixteen of these clutches (59%) were lost as a result of competition for the nest-site with other species, mainly the Southern House Wren *Troglodytes musculus* ($n = 9$) and, to a lesser extent, with the Saffron Finch *Sicalis flaveola* ($n = 4$) and the Bay-Winged Cowbird *Molothrus = Agelaioides badius* ($n = 3$). Of the remaining 13 clutches, six were deserted during cold and rainy weather and one after brood parasitism by Shiny Cowbirds (*Molothrus bonariensis*); two clutches never developed embryos, three failed during hatching and, finally, one incubating female was found dead inside the nest without signs of injury.

At the nestling stage, the Swallows lost seven breeding attempts. Poor weather conditions were the major source of complete nest failure during this stage ($n = 4$ nests); other causes were brood parasitism by Shiny Cowbirds ($n = 1$), nestling starvation unrelated to bad weather ($n = 1$) and nest usurpation after infanticide, probably by Saffron Finches ($n = 1$).

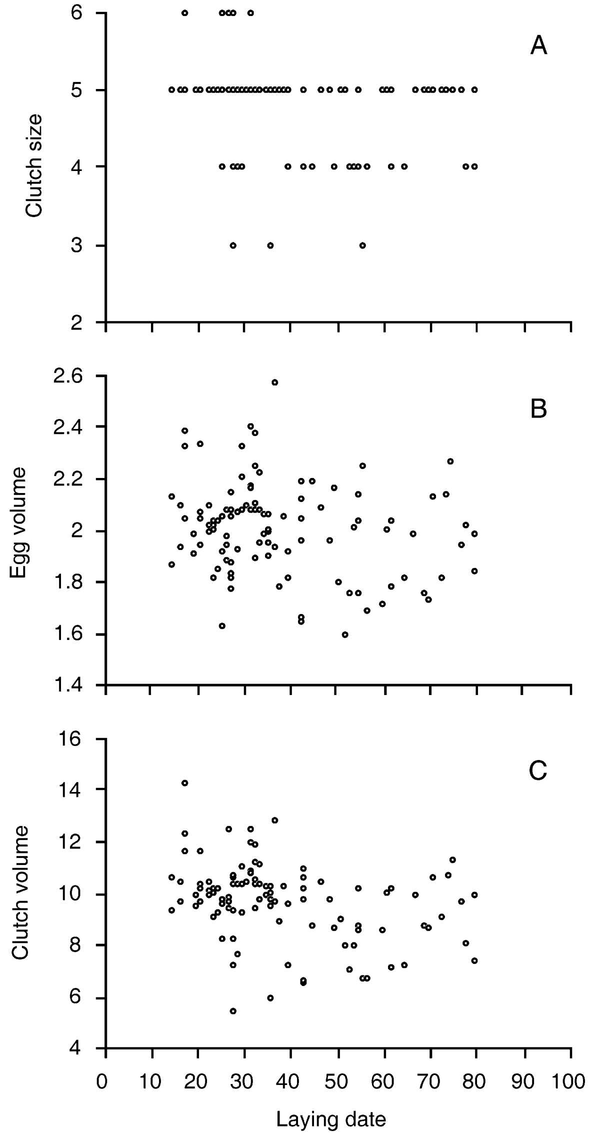

Figure 3. Seasonal decline of clutch size (A), average egg volume (cm^3) (B), and clutch volume (cm^3) (C). Day 0 corresponds to September 15.

Relationship of variables with time of the breeding season

We found a significant decline in clutch size of first clutches as the season progressed (Spearman $r = -0.3$, $n = 105$, $P < 0.001$, Fig. 3A), but this reduction was not detected in second clutches where the sample size was much smaller (Spearman $r = -0.36$, $n = 12$, $P = 0.24$). Average egg length did not change with date of egg-laying (linear regression $R^2 = 0.02$, $df = 1{,}127$, $F = 2.05$, $P = 0.15$), but egg width decreased as the season progressed ($R^2 = 0.03$, $df = 1{,}127$, $F = 4.45$, $P = 0.03$), as did egg weight, although this relationship was not statistically significant ($R^2 = 0.04$, $df = 1{,}72$, $F = 3.41$, $P = 0.07$). The average egg volume also decreased through the breeding season ($R^2 = 0.05$, $df = 1{,}102$, $F = 4.89$, $P = 0.03$, Fig. 3B), as did the volume of the clutch ($R^2 = 0.1$, $df = 1{,}102$, $F = 10.88$, $P = 0.002$, Fig. 3C).

Egg survival increased significantly with date of egg-laying in 2004/05 (Spearman $r = 0.38$, $n = 48$, $P = 0.008$) and in all years combined (Spearman $r = 0.25$, $n = 85$, $P = 0.02$), but neither the length of the incubation period (Spearman $r = -0.05$, $n = 80$, $P = 64$) nor hatching success did so (Spearman $r = 0.13$, $n = 79$, $P = 0.23$). A logistic regression applied to analyse the effect of egg-laying date on hatching asynchrony showed no differences in the pattern of egg hatching (synchronous vs. asynchronous) as the season progressed ($\chi^2 = 2.73$, $df = 1$, $P = 0.10$).

The number of nestlings hatched in a brood did not change through the season (Spearman $r = -0.09$, $n = 69$ nests, $P = 0.46$), but fledgling success increased slightly as the season progressed, although this relationship was not significant (Spearman $r = 0.22$, $n = 69$, $P = 0.07$). The nestling period, calculated for the 2004/05 field season only, decreased as the season progressed (Spearman $r = -0.40$, $n = 43$, $P = 0.007$), from 25 days on average at the beginning of the season to 21 days on average at the end (Fig. 4A). Late-season nestlings spent less time in the nest but their fledgling success was equal to that of early nestlings. In order to investigate whether this relationship could be due to the chicks reaching the asymptotic weight more quickly and leaving the nest in good condition or, conversely, by them leaving in advance at a lower weight, we analysed the daily average weight of chicks through the breeding season. The weight of chicks from day 0–12 did not change with egg-laying date, but late-season nestlings were lighter in weight at day 15 than were early-season nestlings (Spearman $r = -0.35$, $n = 47$, $P = 0.015$, Fig. 4B). As we found no dead chicks in the nests in our daily visits, late-season nestlings must have managed to fledge, even though they might have weighed less than those fledged early in the season.

A logistic regression was used to analyse nest survival (1 or 0) through the season and its relationship with two independent variables, egg-laying date and whether females had been captured or not (2004/05). The whole model showed a significant increment of nest survival as the season progressed ($\chi^2 = 9.33$, $df = 2$, $P = 0.009$), which was explained by the effect

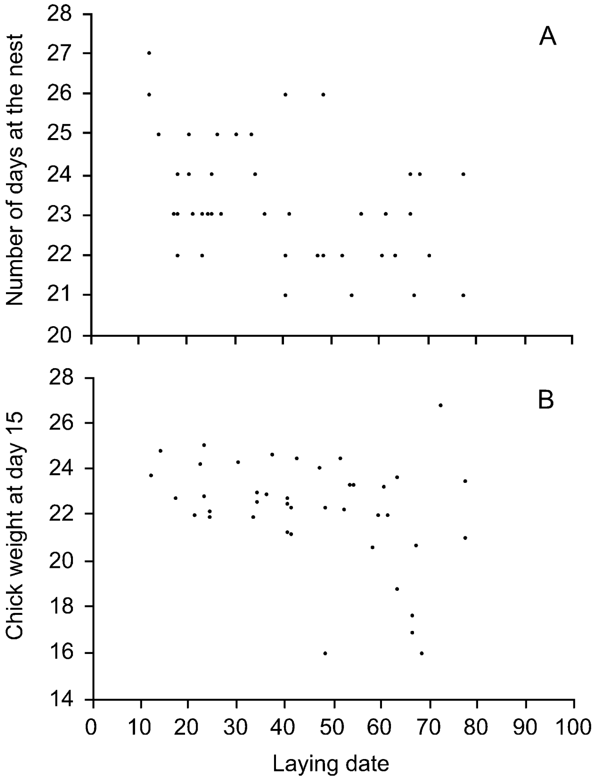

Figure 4. Seasonal decline of the nestling period (A), and chick weight at day 15 (B). Day 0 corresponds to September 15.

of egg-laying date ($\chi^2 = 5.27$, $P = 0.02$) but not by adult capture ($\chi^2 = 0.065$, $P = 0.80$).

DISCUSSION

This study provides detailed information on the breeding biology of one of the least studied species of the genus *Tachycineta*, and allows comparison of some life-history parameters with those of the Tree Swallow. Previous observations of the White-rumped Swallow's nesting behaviour reported them to be highly aggressive solitary nesters (Sclater & Hudson 1889), but even though chases and 'hole perching' behaviour to defend the nestbox entrance from intruders were frequently observed, pairs usually bred within 30 m of each other at Chascomús. The length of the breeding season was 1.5 months longer than that reported by Mason (1985), who found ten nests at Magdalena, Buenos Aires.

Tree Swallows are usually single brooded, only occasionally laying a second brood (Hussell 1983). Similarly, White-rumped Swallows raised one brood per season, although during 2004/05 we determined that 5% of nesting attempts were true second broods, and successful ones. Food supply and length of the breeding season may affect the decision to lay a second clutch. We did not measure the first of these factors, and both species breed over a 5-month period (May–September for Tree Swallows). Therefore, with the available data, there is no apparent reason to expect different levels of double brooding. Only 10% of nesting attempts by the southern species represented replacement clutches but, as it was not feasible to follow the individuals that left the study area following nest failure, our data represent a conservative estimate of the re-laying capacity of the species. In Tree Swallows, 41% of females whose first clutch was experimentally removed laid a replacement clutch (Rooneem & Robertson 1997).

The average clutch size in our study population was less than one egg smaller than that reported for Tree Swallows (Zach 1982, Ramstack *et al.* 1998, Murphy *et al.* 2000); the eggs were around 7% larger (Robertson *et al.* 1992), and between 8 and 11% heavier (Ramstack *et al.* 1998, Whittingham & Dunn 2001). In White-rumped Swallows, egg mass relative to that of the female was 6% greater than had been reported for its northern congener (Ramstack *et al.* 1998).

The incubation period was similar to that reported for Tree Swallows (14.5 days on average, Robertson *et al.* 1992), but hatching success of the southern species was 7–10% poorer (Rendell & Robertson 1993). Hatching spread took up to 4 days, but 58% of the broods hatched synchronously, whereas only 8.6% of the broods of Tree Swallows did so (Zach 1982). White-rumped Swallow nestlings reached peak mass 3–4 days later, had a growth rate 10% less, and remained in the nest 2 days longer than Tree Swallow nestlings (McCarty 2001). White-rumped Swallow nesting success was markedly less than the 76% average reported by Butler (1988) for Tree Swallows. Food availability, a possible source of egg desertion, is unknown at our study site; the major source of nest mortality at Chascomús was interspecific competition for nest-sites during the egg stages, followed by nestling mortality during poor weather.

As in many other species, including the Tree Swallow (Stutchbury & Robertson 1988, Winkler & Allen 1996), clutch size declined as the season progressed. In addition, late-season eggs were smaller and late-season nestlings had a shorter nestling period and lower weight at day 15, probably leaving the nest lighter in weight than had early-season nestlings. These data could indicate that the parents are forcing earlier fledging due to a decline in food availability as the season progresses. However, as we did not know the age and condition of reproductive adults, we cannot yet evaluate their influence on this species.

In Tree Swallows, heavier nestlings are more likely to return the next year (McCarty 2001) and, if the same is found in the White-rumped Swallow, they would benefit greatly from laying early in the season, so providing the nestlings with better survival prospects as in the Tree Swallow (Winkler & Allen 1996). In addition, early White-rumped Swallow breeders may even raise a second brood. However, both major sources of nest mortality, competition for nest-sites with Southern House Wrens and cold and wet weather, decreased through the season. So, even though White-rumped Swallows may benefit from laying early in the season, this effect might be counteracted in part by the increased incidence of nest competition and poor weather during that period.

In summary, White-rumped Swallows follow the pattern found for other southern species, in that they have smaller clutches, lower growth rates and remain longer at the nest than do their Northern Hemisphere congener (Yom-Tov *et al.* 1994, Martin 2002). Future studies on the effect of food abundance, parental care, juvenile and adult mortality, age, and senescence on reproductive output would greatly contribute to characterizing the life-history traits of this relatively unknown swallow. This would improve our understanding of the proximate and ultimate causes that shape life-history traits of species in the genus *Tachycineta*.

We are indebted to David Winkler who enticed us to study this species and to join the Golondrinas de las Américas network, and to G. Somoza and L. Miranda who provided logistic support at the InTeCh-CONICET. This study was made possible by a UBACyT grant X-158 to J.C.R. and by a Ubacyt X-140 grant to V.M. J.C.R. and V.M. are Research Fellows of CONICET, Argentina. F.B. is a doctoral candidate at the same institution.

REFERENCES

Allen, P.E. 1996. Breeding biology and natural history of the Bahamas Swallow. *Wilson Bull.* **108**: 480–495.

Ashmole, N.P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* **103**: 458–473.

Bulit, F. & Massoni, V. 2004. Arquitectura de los nidos de la Golondrina Ceja Blanca *Tachycineta leucorrhoa* construidos en cajas nidos. *Hornero* **19**: 69–76.

Butler, R.W. 1988. Populations dynamics and migration routes of Tree Swallows, *Tachycineta bicolor*, in North America. *J. Field Ornithol.* **59**: 395–402.

Crick, H.Q.P., Gibbons, D.W. & Magrath, R.D. 1993. Seasonal changes in clutch size in British birds. *J. Anim. Ecol.* **63**: 263–273.

De la Peña, M.R. 1996. *Ciclo reproductivo de las Aves Argentinas*. Segunda Parte. Buenos Aires: L.O.L.A.

Dyrcz, A. 1984. Breeding biology of the Mangrove Swallow *Tachycineta albilinea* and the Grey-breasted Martin *Progne chalybea* at Barro Colorado Island, Panama. *Ibis* **126**: 59–66.

Gosler, A.G., Higham, J.P. & Reynolds, S.J. 2005. Why are birds' eggs speckled? *Ecol. Lett.* **8**: 1105–1113.

Hochachka, W. 1990. Seasonal decline in reproductive performance in Song Sparrows. *Ecology* **71**: 1279–1288.

Hussell, D.J.T. 1983. Tree Swallows pairs raise two broods in a season. *Wilson Bull.* **95**: 470–471.

Jones, J. 2003. Tree Swallows *Tachycineta bicolor*: a new model organism? *Auk* **120**: 591–599.

Manning, T.H. 1979. Density and volume correlations of eggs of seven passerine birds. *Auk* **96**: 207–211.

Martin, T.E. 1996. Life history evolution in tropical and south temperate birds: what do we really know? *J. Avian Biol.* **27**: 263–272.

Martin, T.E. 2002. A new view for avian life history evolution tested on an incubation paradox. *Proc. R. Soc. Lond. B* **269**: 309–316.

Martin, T.E. 2004. Perspectives in Ornithology. Avian life-history evolution has an eminent past: does it have a bright future? *Auk* **121**: 289–301.

Martin, T.E., Martin, P.R., Olson, C.R., Heidinger, B.J. & Fontaine, J.J. 2000. Parental care and clutch sizes in North and South American birds. *Science* **287**: 1482–1485.

Mason, P. 1985. The nesting biology of some passerines of Buenos Aires, Argentina. In Buckley, P.A., Foster, M.S., Morton, E.S., Ridgely R.S. & Buckley, F.G. (eds) *Neotropical Ornithology*: 954–972. Washington, DC: AOU.

McCarty, J.P. 2001. Variation in growth of nestling Tree Swallows across multiple temporal and spatial scales. *Auk* **118**: 176–190.

Moore, O.R., Stutchbury, B.J.M. & Quinn, J.S. 1999. Extra pair mating system of an asynchronously breeding tropical songbird, the Mangrove Swallow. *Auk* **116**: 1039–1046.

Moreno, J., Merino, S., Vásquez, R.A. & Armesto, J.J. 2005. Breeding biology of the Thorn-tailed Rayadito (Furnariidae) in south-temperate rainforest of Chile. *Condor* **107**: 69–77.

Murphy, M.T. 1986. Temporal components of reproductive variability in Eastern Kingbirds (*Tyrannus tyrannus*). *Ecology* **67**: 1483–1492.

Murphy, M.T., Armbrecth, B., Vlamis, E. & Pierce, A. 2000. Is reproduction by Tree Swallows cost free? *Auk* **117**: 902–912.

Pereyra, J.A. 1969. Avifauna Argentina. Familia Hirundinidae: Golondrinas. *Hornero* **11**: 1–19.

Perrins, C.M. & McCleery, R.H. 1989. Laying dates and clutch size in the Great Tit. *Wilson Bull.* **101**: 236–253.

Quinney, T.E., Hussell, D.J.T. & Ankney, C.D. 1986. Sources of variation in growth of Tree Swallows. *Auk* **103**: 389–400.

Ramstack, J.M., Murphy, M.T. & Palmer, M.R. 1998. Comparative reproductive biology of three species of Swallows in a common environment. *Wilson Bull.* **110**: 233–243.

Rendell, W.B. & Robertson, R.J. 1993. Cavity site, clutch-size and the breeding ecology of Tree Swallows *Tachycineta bicolor*. *Ibis* **135**: 305–310.

Ricklefs, R.E. 1967. A graphical method of fitting equations to growth curves. *Ecology* **48**: 978–983.

Ridgely, R.S. & Tudor, G. 1989. *The Birds of South America*, Vol. 1. Oxford: Oxford University Press.

Robertson, R.J., Stutchbury, B.J. & Cohen, R.R. 1992. Tree Swallow. In Pool, A., Stettenheim, P. & Gill, F. (eds) *The Birds of North America*, No. 11. Philadelphia: The Academy of Natural Sciences, and Washington, DC: The American Ornithologists' Union.

Rooneem, T.M. & Robertson, R.J. 1997. The potential to lay replacement clutches by Tree Swallows. *Condor* **99**: 228–231.

Russell, E.M., Yom Tov, Y. & Geffen, E. 2004. Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. *Behav. Ecol.* **15**: 831–838.

Sclater, P.L. & Hudson, W.H. 1889. *Argentine Ornithology*, Vol. 1. London: Porter.

Skutch, A.F. 1985. Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. In Buckley, P.A., Foster, M.S., Morton, E.S., Ridgely, R.S. & Buckley, F.G. (eds). *Neotropical Ornithology*: 575–594. Washington, DC: AOU.

Stutchbury, B.J. & Robertson, R.J. 1988. Within-seasonal and age-related patterns of reproductive performance in female Tree Swallows *Tachycineta bicolor*. *Can. J. Zool.* **66**: 827–834.

Turner, A. & Rose, C. 1989. *Swallows and Martins of the World*. London: A. & C. Black.

Whittingham, L.A. & Dunn, P. 2001. Female responses to intraspecific brood parasitism in the Tree Swallow. *Condor* **103**: 166–170.

Winkler, D. & Allen, P.E. 1996. The seasonal decline in Tree Swallows clutch size: physiological constraint or strategic adjustment? *Ecology* **77**: 922–932.

Yom-Tov, Y., Christie, M.I. & Iglesias, G.J. 1994. Clutch size in passerines of Southern South America. *Condor* **96**: 170–177.

Zach, R. 1982. Hatching asynchrony, egg size, growth, and fledging in Tree Swallows. *Auk* **99**: 695–700.

Zach, R. & Mayoh, K.R. 1982. Weight and feather growth of nestling Tree Swallows. *Can. J. Zool.* **60**: 1080–1090.

Received 21 September 2005; revision accepted 28 March 2006.