Time of breeding and female condition affect chick-growth in the Chilean Swallow (*Tachycineta meyeni*)

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Abstract. We analysed growth of nestling Chilean Swallows (*Tachycineta meyeni*) over four consecutive breeding seasons and determined the factors that explain variation in growth rate, asymptotic body mass and length of the nestling period. As the breeding season advanced nestlings grew more slowly and attained lower asymptotic mass, but the length of the nestling period and nestling survival did not show any seasonal trend. Asymptotic body mass of nestlings increased with female body condition, which was negatively correlated with time of breeding, suggesting that a seasonal decline in asymptotic body mass could be the result of changes in environmental conditions or lower quality of females breeding later in the season. There was no relationship between average minimum ambient temperature and either growth rate or asymptotic mass during the nestlings first 10 days. However, short periods of poor weather and snowfall had a significant effect on nestling survival. Growth rate (0.43) was lower than that of other *Tachycineta* species nesting at similar latitudes in the northern hemisphere but similar to those of subtropical species of the genus, suggesting that the factors that have influenced the evolution of this life-history trait differ between Chilean Swallows and other species of *Tachycineta*.

Introduction

In some *Tachycineta* swallows, the growth rate of nestlings declines as the breeding season progresses (McCarty and Wikler 1999; Massoni *et al.* 2007). This decline may be related to lower parental quality of late breeders (Price *et al.* 1988) or to seasonal trends in the environment (Lack 1966) or a combination of both. The body condition of the female parent can also have an effect on nestling growth because females in better condition require fewer resources for their own self-maintenance and can allocate more resources to their offspring than those in poor condition (Newbrey and Reed 2009). Short-term changes in environmental conditions can also affect nestling growth and survival (McCarty and Wikler 1999; Eeva *et al.* 2002). Temperature has a direct effect on growth rate by affecting the metabolic demands on developing chicks (McCarty and Wikler 1999) and an indirect effect by regulating food supply (Bryant 1975). This is particularly important for aerial insectivores, as lower temperatures may ground insects making them unavailable to aerial foragers (Bryant 1975; McCarty and Wikler 1999).

The Chilean Swallow (*Tachycineta meyeni*) offers an excellent model to examine factors that influence nestling growth. It is the species with the most southerly distribution within its genus and breeds in an environment where ambient temperature during the breeding season can reach below 0°C. Furthermore it is an obligate aerial insectivore which makes it vulnerable to decreases in the supply of food owing to low ambient temperatures.

In this study we analyse the effect of time of breeding, female condition and ambient temperature on variation in nestling growth rate and asymptotic mass and the length of the nestling period in Chilean Swallows. We also provide information on nestling survival and compare the main reproductive parameters of Chilean Swallows with those available for other species of the genus *Tachycineta*. We expect that growth rate and asymptotic mass of nestlings are negatively associated with time of breeding, and positively associated with female body condition and with ambient temperature. Also, considering the general pattern of positive correlation between latitude and growth rate (McCarty 2001; Remeš and Martin 2002), we expect Chilean Swallows to have a higher growth rate than species of the same genus nesting at lower latitudes, and similar rates to that of species nesting at a similar latitude in the northern hemisphere.

Materials and methods

Study site and data collection

We studied Chilean Swallows breeding in nest-boxes at three sites near the city of Ushuaia, Tierra del Fuego, Argentina. Site A (54°44′S, 68°12′W) was 15 km north-east of Ushuaia, site B (54°44′S, 67°54′W) 40 km east of Ushuaia, and site C (54°53′S, 67°20′W) 85 km east of Ushuaia. Chilean Swallows are austral migrants that remain in our study area from October to March. Laying occurs from late October to early January and the last chicks fledge in mid-February. They are typically single-brooded

and only one second brood was recorded during our study. To facilitate data collection we set up 88, 68 and 62 nest-boxes at sites A, B and C. Nest-boxes were placed in trees or on fence posts at a height of 1.5 m and separated by at least 20 m. External dimensions of the boxes were $25.4 \times 16.5 \times 17.8$ cm (height, width, depth), whereas internal dimensions were $23.8 \times 12.7 \times 12.7$ cm. Boxes had a 3.5-cm diameter entrance hole and a lateral opening that allowed us to monitor the progress of the nest. Boxes were placed with the entrance hole facing N, NE or E as predominant winds in our study site come from the SW. The study was conducted during the breeding seasons (October–February) of 2006–07, 2007–08, 2008–09 and 2009–10.

We began monitoring nest-boxes in mid-October and visited nests every other day during nest-construction, daily during laying, every 2 days during incubation and daily near the expected day of hatching. We individually marked nestlings with nail polish applied to their toe-nails the day of hatching and with a numbered aluminium ring at 12 days of age. During visits all nestlings were weighed with Pesola spring balances (10 ± 0.1 g and 30 g ± 0.2 g) on the day of hatching (Day 0) and when nestlings were 3, 6, 9, 12, 15 and 18 days old. After chicks were 18 days old we monitored nests non-invasively without removing the nestlings from the nest-box to avoid premature fledging. The length of the nestling period was defined per brood and was calculated as the number of days between the hatching of the first nestling to the fledging of the last nestling ($n = 92$ nests, 87 first clutches and five replacement clutches, in which all nestlings fledged successfully). Within the first 6 days after hatching we captured and banded the nesting female. Females were not captured earlier because the probability of abandonment of nests after capture is higher during incubation. During captures we measured head-bill length with a dial calliper (error ± 0.1 mm; Mitutoyo Corporation, Kawasaki, Japan), wing-length using a stopped wing-rule (error ± 0.5 mm) and body mass with a Pesola spring balance (30 ± 0.2 g). Our manipulations did not have any significant effect on the reproductive success of Chilean Swallows (i.e. desertion of nests) and comply with the laws of Argentina and the province of Tierra del Fuego.

We obtained data on ambient temperature from the Environmental and Geographic Information Service of the Centro Austral de Investigaciones Científicas (CADIC) in Ushuaia. We used data from two weather stations, one in the city of Ushuaia (used for sites A and B), and the other 15 km away from site C. These stations recorded ambient temperature every hour. For each nest we calculated the mean minimum daily temperatures during the first 10 days of the nestling stage.

Data analysis

For each nest we calculated nestling survival, as the number of nestlings fledged divided by the number of nestlings hatched. For this calculation we included abandoned nests where no nestlings fledged. We recorded the most probable cause of nestling loss as: (1) abandonment (all nestlings were dead in the nest) and (2) predation (all nestlings disappeared from the nest between consecutive visits). We estimated nestling growth curves from data recorded in 94 nests (89 first clutches and 5 replacement clutches, in which all nestlings fledged successfully, $n = 296$ chicks). We did not include data from nests with brood reduction

because chicks that die from starvation or hypothermia may show atypical growth curves. We used non-linear regressions and least-squares procedures (in software CurveExpert, see www.curveexpert.net, accessed 5 April 2012) to fit logistic growth curves of the form:

$$y = a/(1 + be^{-Kx})$$

to the masses of each chick, where x refers to the nestling age, y is the body mass at age x, a is the asymptotic body mass, K is the growth rate constant of the logistic regression and b the inflection point (Ricklefs 1968). Because nestlings within a nest are not independent, we calculated the mean parameters of the growth curve for each nest and used these mean values in the analysis ($n = 94$ nests).

To examine possible factors explaining the variation in asymptotic mass (a), growth rate (K) and length of the nestling period we used general linear mixed models (GLMM) from the statistical package R (Version 2.13.1, R Development Core Team 2009; also see Crawley 2007). For the asymptotic mass and the growth constant we used GLMM with Gaussian family distribution and identity link function, whereas for the length of the nestling period we used GLMM with Poisson family distribution and log-link function (Crawley 2007). Each model contained the following fixed effects: day of hatching, female body condition, average minimum ambient temperature during the first 10 days of nestlings life and number of hatchlings. We also included breeding season as a random term. For laying date we considered 1 October as the first day of the breeding season and all dates are reported relative to that day. We used residual body mass of females, calculated as the residuals of the regression of body mass against head-bill length (Ardia 2005), as an index of female body condition. To simplify the maximal model we used a backward stepwise procedure, removing the least significant terms first and retaining only the significant explanatory variables.

All tests are two-tailed with P set at 0.05. We present data as means $\pm$ standard errors and we included the median for variables that did not follow a normal distribution.

Results

Nestling growth

The main growth parameters of Chilean Swallows are presented in Table 1. Mean body mass at hatching (Day 0) was 1.8 ± 0.03 g (median 1.8 g, $n = 64$ nests) and the estimated asymptotic body mass was 21.7 ± 0.2 g ($n = 94$ nests). Growth rate and asymptotic mass decreased as the season progressed (growth constant: $\beta = -0.001 \pm 0.0005$; asymptotic mass: $\beta = -0.046 \pm 0.016$; Table 2; Fig. 1*a, b*). Growth rate decreased with female body condition ($\beta = -0.0006 \pm 0.0002$; Table 2) whereas asymptotic mass increased ($\beta = 0.019 \pm 0.008$; Table 2). Average minimum ambient temperature during the first 10 days of age of the chicks and brood size were not related to variation in growth rate or to asymptotic mass (Table 2). We repeated the analysis with maximum instead of minimum ambient temperature and the results were quantitatively similar. Female body condition was negatively correlated with day of hatching (Spearman rank correlation $r = -0.3$, $P = 0.006$). On average, the length of the nestling period was 26 ± 0.2 days (median 26, range 21–34,

Table 1. Mass at hatching, nestling growth rate and asymptotic body mass, length of the nestling period and nestling survival for Chilean Swallows nesting in Tierra del Fuego, Argentina, during four breeding seasons

Values are means ± s.e.; *n* (sample size) is the number of nests. Nestling survival was calculated as the number of nestlings fledged divided by the number of nestlings hatched

Season	Mass at hatching (g)	Growth rate (g day^{-1})	Asymptotic mass (g)	Nestling period (days)	Nestling survival
2006–07	1.8 ± 0.1 (*n* = 18)	0.42 ± 0.02 (*n* = 17)	22.3 ± 0.4 (*n* = 17)	25.9 ± 0.6 (*n* = 17)	0.74 ± 0.09 (*n* = 23)
2007–08	1.7 ± 0.1 (*n* = 25)	0.41 ± 0.01 (*n* = 37)	22.3 ± 0.3 (*n* = 37)	25.7 ± 0.3 (*n* = 37)	0.95 ± 0.03 (*n* = 39)
2008–09	1.7 ± 0.1 (*n* = 32)	0.44 ± 0.02 (*n* = 13)	20.8 ± 0.6 (*n* = 13)	27.5 ± 0.8 (*n* = 13)	0.32 ± 0.06 (*n* = 48)
2009–10	1.7 ± 0.1 (*n* = 25)	0.45 ± 0.01 (*n* = 27)	20.9 ± 0.4 (*n* = 27)	25.7 ± 0.3 (*n* = 27)	0.85 ± 0.05 (*n* = 35)

Table 2. Factors affecting growth rate and asymptotic mass of nestling Chilean Swallows during the breeding seasons 2006–07 to 2009–10 in Tierra del Fuego, Argentina

Denominator degrees of freedom presented in the table (d.f.); numerator degrees of freedom 1 for all tests

Effect	d.f.	*F*	*P*
Growth rate			
Day of hatching	86	5.6	0.02
Female body condition	86	5.1	0.03
Temperature	86	0.4	0.55
Brood size	86	0.5	0.50
Asymptotic mass			
Day of hatching	86	12.5	0.0007
Female body condition	86	5.9	0.02
Temperature	86	1.1	0.29
Brood size	86	2.4	0.12

n = 94 nests). Day of hatching, female body condition, temperature during the first 10 days of age and brood size were not related to variation in length of the nestling period (all $P > 0.05$).

Nestling survival

Of the 145 nests in which at least one chick hatched, 72% (*n* = 104) were successful (at least one chick fledged), 24% (*n* = 35) were abandoned (all nestlings were found dead) and 4% (*n* = 6) were depredated. In abandoned nests, the minimum average daily temperature during the 2 days before the death of nestlings was significantly lower than the minimum average daily temperature experienced by nestlings from successful nests during their first 10 days of age (2.5 ± 0.4°C, *n* = 35 v. 4.9 ± 0.1°C, *n* = 104, $t_{38} = -6.31$, $P < 0.001$).

Nestling survival was 0.68 ± 0.03 (median 1, range 0–1, *n* = 145 nests) and varied between breeding seasons (Kruskal–Wallis test: $H_3 = 48.78$, $P < 0.0001$) being lowest in 2008–09, a season when 68 of 76 chicks <12 days of age (*n* = 23 nests) died during 2 days of poor weather and snowfall in late December. During these two days, 13 of 13 chicks >12 days old (*n* = 4 nests) survived. These days the minimum daily temperature was 0.3°C, compared with the minimum daily average of 5.1°C recorded for the rest of December. Nestling survival did not vary with day of hatching (Spearman correlation: $P > 0.05$ in all four breeding seasons). If we only consider nests at which at least one chick fledged, nestling survival was 0.96 ± 0.01 (median 1, range 0.3–1, *n* = 104 nests).
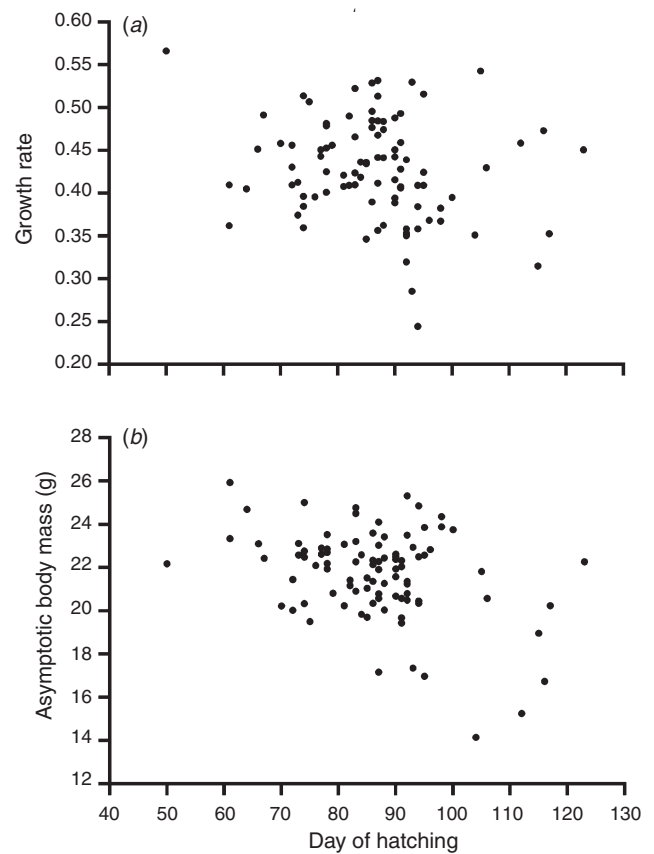

Fig. 1. Relationships between (*a*) nestling growth rate and day of hatching during the breeding season and (*b*) asymptotic body mass and day of hatching during the breeding season. Data are means of 94 nests in which all chicks fledged successfully from the breeding seasons 2006–07 to 2009–10 in Tierra del Fuego, Argentina. Day of hatching is expressed as days elapsed since October 1 (Day 0).

Discussion

As the breeding season advanced, nestling Chilean Swallows grew more slowly and attained a lower asymptotic mass, but the length of the nestling period and nestling survival did not show any significant seasonal variation. The negative influence of time of breeding (day of hatching) on nestling growth is consistent with results reported for other species of swallows. In Tree Swallows (*T. bicolor*) hatching date has a negative effect on nestling mass-gain independently of insect abundance and tem-

perature, probably because parents breeding later in the season provide lower quality parental care (McCarty and Wikler 1999). Similarly, in White-rumped Swallows (*T. leucorrhoa*) there is a seasonal decrease in nestling mass at 15 days of age (Massoni *et al.* 2007). The seasonal decline in nestling growth could be the result of lower quality of females that breed late in the season (Winkler and Allen 1996; Ardia and Clotfelter 2007). Consistently, we found that the body condition of females decreased with time of breeding and that nestlings of females with better body condition reached a greater asymptotic mass. However, we also found that nestlings of females with better body condition grew more slowly, which suggests a possible trade-off between growth rate and asymptotic mass. Nestlings with female parents in better condition may also not have been fed as much as those fed by females of lesser condition. Future work recording feeding rates of females and examining whether feeding rate is lower by females in better condition will help elucidate this possible trade-off. In addition to differences in female quality, we cannot exclude an environmental effect, as resources may decrease over the duration of the breeding season resulting in lower condition of females and their offspring later in the breeding season. Future experimental manipulations are needed to separate the effects of individual variation and environmental changes.

Average minimum ambient temperature during the first 10 days of nestling life did not have a significant effect on the growth-rate constant or the asymptotic mass of nestlings that survived, which suggests that Chilean Swallows may have evolved to deal with low temperatures (e.g. $\leq 5°C$) over the nestling period. McCarty and Wikler (1999) examined the effects of shorter term changes (day-to-day) in environmental conditions (food, wind and ambient temperature) on the growth of nestling Tree Swallows. In their study, ambient temperature (measured as maximum daily temperature) had the greatest influence on the change in body mass (2 days apart) of nestlings <5 days old, whereas for nestlings >9 days old, availability of food and temperature were equally important (McCarty and Wikler 1999). In our study we analysed the effect of temperature at a greater temporal scale (10 days) and integrated the entire growth period (growth-rate constant and asymptotic mass), which could have masked possible effects of temperature on growth at a smaller temporal scale.

Conversely, the very low nestling survival recorded in the 2008–09 breeding season, when most nestlings died during a short period of poor weather and snowfall in late December, and the below average minimum daily temperature (near 0°C) experienced in nests where all nestlings died suggests that sudden and extreme fluctuation in weather conditions on a small temporal scale have an important effect on nestling survival. Our results suggest that Chilean Swallows in our study population are able to cope with cold weather, which could be adaptive given the high probability of cold weather at the time of breeding in this high-latitude study site (Eeva *et al.* 2002). However, their response to unpredictable temporal fluctuations, such as a cold spell during the nestling period, seems more limited, resulting in a dramatic decline in their reproductive success. Several studies have shown the effect of low temperatures on food abundance and growth of chicks of aerial insectivores (Bryant 1975, 1978; Quinney *et al.* 1986; McCarty and Wikler 1999). Studies on the effect of low temperatures on insect abundance at the breeding sites of Chilean Swallows and estimation of the provisioning rates by parents may help to understand better the relative importance of sudden changes in environmental variables on female condition and nestling growth in this species.

Although all species of *Tachycineta* are aerial insectivores, their growth rates show certain variability with latitude. In our study Chilean Swallows breeding at 54°44′S had a growth constant of 0.43 (range 0.41–0.45). Other values of growth constants for species of this genus are: 0.41 for Violet-green Swallows (*T. thalassina*) breeding at 48°40′N (Edson 1943, in McCarty 2001); 0.53 (range 0.49–0.56) for Tree Swallows breeding at 42°30′N (McCarty 2001); 0.46 for White-rumped Swallows breeding at 35°34′S (Massoni *et al.* 2007); 0.36 for Bahama Swallow (*T. cyaneoviridis*) breeding at 26°40′N (Allen 1996); and 0.42 for Mangrove Swallow (*T. albilinea*) breeding at 8°31′N (Ricklefs 1976). McCarty (2001) compared the nestling growth constants (K) of 16 species in the family Hirundinidae (including Violet-green, Tree, Bahama and Mangrove Swallows) and found that species breeding closer to the Equator had slower growth rates than species breeding at higher latitudes, which supports the general pattern of slow growth in tropical species (Ricklefs 1968, 1976). Contrary to what we expected according to this latitudinal pattern, the growth constant of Chilean Swallows seems more similar to that reported for subtropical species (and also for Violet-green Swallows). One possible explanation for these results is that extreme heat has a similar effect as extreme cold on the ability to forage on insects, either because insects may avoid being in the air during extremely hot and dry conditions or because with high ambient temperatures swallows are under heat stress and cannot sustain hunting flight for long periods. Further studies on other species of *Tachycineta* breeding at sites with extreme climate conditions are needed to elucidate the generality of latitudinal variation in growth rate in this genus.

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