



# Insights into life history theory: a brood size manipulation on a southern hemisphere species, *Tachycineta leucorrhoa*, reveals a fast pace of life

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Life history traits exhibit substantial geographical variation associated with the pace of life. Species with a slow pace are expected to invest more in their future/residual reproductive value and are more common at tropical latitudes, whereas species from high latitudes, with a faster pace, are expected to prioritize the current reproductive effort. Most evidence supporting this pattern comes from studies conducted in tropical and north temperate species; very little is known about patterns in southern South American species. Here, we describe the life history of a southern swallow *Tachycineta leucorrhoa* and use an experimental approach to test their breeding strategy over four breeding seasons. We manipulated brood size for 105 nests of white-rumped swallows to measure whether costs of reproduction were borne by adults or nestlings as alternative selection strategies towards maintaining residual or current reproductive value. Adults increased their feeding effort in enlarged broods, at least enough to maintain nestlings' development/growth. In addition, adults decreased the number of visits to the nest (without having a negative effect on nestlings) in reduced broods. We did not detect differences in fledging success among treatments, suggesting there were no differences in nestlings' survival. However, enlarged broods more frequently incurred in complete nest failure, suggesting only some adults were able to cope with increased costs of reproduction. We conclude this species is characterized by a fast pace of life similar to their northern congeners and less like its tropical ones. This is one of the first studies to use an experimental approach to test a life history hypothesis of pace of life using data from a southern South American species. We encourage researchers to include southern species when evaluating latitudinal variations as we still do not have enough evidence to assume all southern subtropical species are indeed similar to tropical ones.

Life history traits are traits that can affect reproduction and survival, and the predominant life history strategy observed in a given population is generally the result of the tradeoffs among different interacting traits that are under natural selection. Life history traits include traits such as the timing of breeding, reproductive effort, offspring survival related to parental effort, and the survival of adults, all characters that contribute directly to fitness (Roff 1992, Stearns 1992). In the last decades, studies on birds have provided a large amount of information on some of these components of fitness. Particularly, fertility, measured as clutch size, is probably one of the most extensively studied traits (Jetz et al. 2008). Other traits that have also been subjects of study in the last decades are the amount of parental care provided to the brood (Cockburn 2006), and survival rates of the adults (Lebreton et al. 1992, McGregor et al. 2007). These traits are not independent from each other; time, nutrients and energy are limiting factors in nature, tradeoffs among them emerge and the outcome may affect

other fitness components. For example, tradeoffs between reproduction and survival (Williams 1966) may affect the parental care provided to the brood (Ghalambor and Martin 2001, Fontaine and Martin 2006) and, consequently, offspring growth rates (Roff 1992, Dmitriew 2011).

Life history traits of birds, from clutch size (Lack 1947, Cardillo 2002, Martin et al. 2006) to adult mortality rate (Brawn et al. 1999, Sandercock et al. 2000), have been documented to change latitudinally, and their geographic variation still drives much of the current research in ornithology (Ruuskanen et al. 2011, Stevens 2011, Jetz et al. 2012). Different hypotheses have been proposed to explain this latitudinal variation. In the Pace of life hypothesis (Ricklefs and Wikelski 2002) two extreme strategies are defined at both ends of a continuum. On one end, a slow pace of life is characterized by high adult survival rates and low parental investment for each reproductive event, evidenced by a small clutch size and slow nestling development (Magrath et al. 2000, Wikelski et al. 2003). On the other

end, a fast pace of life is characterized by low adult survival rates and high parental investment, i.e. large clutch size and fast offspring development (Ghalambor and Martin 2001). These extreme strategies have been associated with different geographic regions with species in the tropics exhibiting a slow strategy and those in the temperate zone a fast strategy. Current studies, some including physiological traits, also support the generalization that pace of life is slower at lower latitudes (Ricklefs and Wikelski 2002, Hau et al. 2010, Williams et al. 2010, Cooper et al. 2011, Martin et al. 2011). However, we believe it is still important to characterize the pace of life for species in latitudes that have not been intensively studied, to obtain a more comprehensive knowledge of the variation of life history traits (Ferretti et al. 2005).

The adaptive outcomes of life history tradeoffs in birds of the South Temperate Zone are still poorly known, especially when compared to those from North Temperate and Tropical areas (Magrath et al. 2000, Barker 2005, Biancucci and Martin 2010, Stevens 2011). The South Temperate Zone refers to the area between the Tropic of Capricorn and the Antarctic Circle, including southern Australia, New Zealand, South Africa, and southern South America. Even though there has been an important progress in our understanding of the biology of the species of this large geographic region in the last decade (Ghalambor and Martin 2001, Martin et al. 2006, Chalfoun and Martin 2007, Martin et al. 2011), the knowledge gained on southern South American species might be obscured by the terminology used to refer to birds inhabiting this region. South America is delimited on the northwest by the Darién Gap, a large swampland and forest that divides the central region of Panama from Colombia. Indeed, southern South American species may be correctly referred to as being Neotropical (e.g. in Ferretti et al. 2005), subtropical (e.g. in Auer et al. 2007) or South Temperate (e.g. in Llambías and Fernandez 2009) birds, following biogeographic, climatic, or ecological definitions, and depending on the comparative analysis the researchers emphasized.

A number of studies have investigated the life history of subtropical South American birds, with some of them conducted very close to the Tropic of Capricorn (Martin et al. 2000, Ghalambor and Martin 2001, Martin et al. 2006, Martin 2008). In these studies, phylogenetically related species from North Temperate latitudes were used to compare life history strategies of both groups of birds. As a result, those Subtropical species examined (i.e. those living close to the tropics) exhibited a great similarity with tropical species but differed from north temperate species. Our previous studies on the white-rumped swallow *Tachycineta leucorrhoa* (Massoni et al. 2007, Bulit et al. 2008, Bulit and Massoni 2011) conducted within the subtropical region (11 degrees south in latitude from the above mentioned studies) showed that life history traits of this species were more similar to those of the northern temperate fast living congener, the tree swallow *Tachycineta bicolor* (Winkler and Allen 1996, Dunn et al. 2000, Ardia 2005), than to those of the tropical or slow living congeners *T. albilinea*, *T. cyaneoviridis*, *T. euchrysea* (Townsend et al. 2008) and *T. stolzmanni* (Stager et al. 2012). Given these contrasting results we wanted to further advance our

understanding of the breeding biology of *Tachycineta leucorrhoa* and used an experimental design, based on a brood size manipulation, to test the predictions made by the pace of life hypothesis.

Enlarged broods can increase the cost of reproduction to the adults, and researchers have used this approach to explore proximate responses or the phenotypic plasticity of individuals (Martin 2004), i.e. their ability or willingness to allocate resources to present or future reproduction. A good way to test this is to evaluate several fitness components simultaneously and measure whether parents react by absorbing the costs of the current reproductive event themselves or whether they pass on the costs to their offspring (Sousa and Marini 2012). If parents accept the extra costs they should experience changes in body condition or survival, reduced re-nesting probabilities or reduced future clutch size. Alternatively, if parents do not face the increased reproductive cost and pass this on to the next generation, a reduced growth rate or nestling survival should be expected (Murphy et al. 2000, Parejo and Danchin 2006, Shutler et al. 2006, Sanz-Aguilar et al. 2008). The combination of this experimental design and the geographic variation in life history strategies' framework leads to the following prediction: species following a slow pace of life with high chances of survival (e.g. those similar to the ones living in tropical latitudes) should pass on more costs to their current young than species following a fast pace of life with lower adult survival and few chances of breeding again (Ghalambor and Martin 2001, Ricklefs and Wikelski 2002, Sousa and Marini 2012).

In the present study we evaluated the response of the southern, subtropical, South American white-rumped swallow to a brood size manipulation designed to increase the cost of current reproduction. This response was evaluated in terms of current reproductive effort by measuring differences in parental behavior, nestlings' development and survival among different treatments, along four breeding seasons. We evaluated the residual reproductive effort after the brood manipulation by measuring the adults' body mass and condition, return rate and reproductive parameters the following season. Finally, with the combined results we characterized the life history strategy of this species and compared it with the strategy of other congeners breeding at different latitudes. This approach allowed us to broaden the discussion about geographic variation of life histories, a debate normally based on gradients between north and central latitudes, by including results from a temperate southern region. In line with our previous findings, white-rumped swallows are expected to display traits and behaviors that would place them closer to the 'fast' end of the life history strategy continuum, with adults absorbing the increased costs of reproduction at the expense of their own survival.

## Methods

We studied white-rumped swallows breeding in a 136 nest-box system from September until January of 2006(2007) to 2009(2010) at the IIB-INTECH-CONICET (for a detailed

site description see Massoni et al. 2007), Buenos Aires Province, Argentina (35°34'S, 58°01'W). This area belongs to the depressed pampas habitat (Soriano 1991) characterized by a subtropical climate with mean annual temperature of 18°C and from 7 to 9°C during the coldest months (Servicio Meteorológico Nacional, Argentina). Boxes were checked daily since the onset of egg laying, during the laying period, and at the end of the incubation period to detect the exact hatch date (i.e. when the majority of the eggs hatch). Clutch size was determined when no new eggs were found at the nest for two or more consecutive days.

We conducted brood size manipulations on the day the eggs hatched during the four breeding seasons previously mentioned. Triads of nests sharing the same hatch date and clutch size were used: two sets of nests were used to transfer randomly selected nestlings between them, while the third group retained the original nestlings (hereafter referred as a control brood). Considering the mean clutch size for this population is five eggs and mean hatchling number is four (Massoni et al. 2007), two or three randomly selected hatchlings were removed from some nests (reduced broods hereafter) and added to other nests (enlarged broods hereafter). Brood size after the manipulation was seven/six, five/four, and three/two hatchlings for enlarged, control and reduced broods, respectively (the number of hatchlings transferred represented approximately a 50% increase). Nests in each triad were chosen to have the same original clutch size to control for potential differences in female quality and/or condition. As the reproductive effort may differ between first and second nesting attempts only first clutches were used for the experiment. Different broods of the same female across seasons were not manipulated on consecutive seasons to avoid imposing the costs of the experiment repeatedly on the same individual.

Eight to nine days after clutch completion females were captured inside the nest-boxes, banded with a uniquely numbered ring, weighed and measured (head plus bill and flattened wing). Males were captured and measured when nestlings were between eight to nine days old and females were recaptured and weighed again on the day after the male was captured (also during the rearing period). This protocol allowed us to measure the difference in females' mass and body condition before and after the experimental manipulation had taken place and males' mass and body condition after having fed enlarged, control or reduced broods for eight to nine days. Two measures of adults' body condition were used: mass and an index of body condition calculated separately for each sex. The morphological variables (head plus bill and flattened wing) were included in a principal components analysis (PCA), the values of the first component of this analysis were regressed against body mass and the residual values of this regression were used as an index of adult body condition. All females whose nests had survived until the onset of incubation and all the males whose nests had reached day eight/nine of the nestling period were measured, banded, and the return rate for each sex within each treatment was estimated [e.g. return rate of females at enlarged broods: number of recaptured females at ( $t + 1$ ) that raised enlarged broods at ( $t$ )/number of females that raised enlarged broods at ( $t$ )].

Starting on hatch day (day 0 hereafter) nestlings were weighed every other day to the nearest 0.1 g during 2006 and to the nearest 0.05 g during 2007–2009 seasons until day 15, after which their handling was avoided to prevent premature fledging. Using non-toxic markers each hatchling received a unique leg mark renewed every other day to ascertain its nest of origin and allow identification during early development. This procedure was repeated until they were banded with uniquely numbered aluminum bands at day 9/10 of age. The nestling period was defined as the time elapsed between the hatch date and the day before all nestlings had fledged at a normal age without signs of predation. All the mortality events, either partial or total loss of the brood due to predation or nest abandonment, were registered. The number of fledged young and the fledging success (the proportion of hatchlings born at that nest that fledged successfully) were registered at each experimental nest.

Nest visitation behavior of males and females was recorded using video cameras when nestlings were four and 12 d old. The sex of adults was distinguished in the field and videos by the presence or absence of temporary marks made with non-toxic markers in the females' breast, abdomen and rump during the first capture. All recordings were made between 07:00 and 14:00 h for two consecutive hours using video recorders placed 20–30 m away from the nest-box entrance. Sample sizes vary among treatments and stages of development because no recordings were made during inclement weather conditions. Videotapes were subsequently analyzed and a feeding rate (number of feeding visits per hour) was estimated for each sex and stage. To explore the parental effort from the nestlings perspective we estimated per nestling feeding rate as the number of feeding visits per hour/number of nestlings on the recording day.

## Data analysis

The difference in mass of hatchlings born at nests that were later enlarged, control or reduced broods was investigated using ANOVA to rule out potential maternal effects that may have resulted in differential egg or hatchling mass at the onset of the experimental treatments (Styrsky et al. 1999).

Differences in feeding visit rates and per nestling feeding rate among treatments were analyzed using Kruskal–Wallis tests. The potential factors affecting nestlings' development were evaluated using generalized linear mixed models (GLMM). Nestlings' mass at day 15 of age was defined as the dependent variable and standardized hatching date, treatment (control, reduced and enlarged brood) and year were included as fixed terms. To control for variation on the hatch date between seasons this variable was standardized by dividing the difference between the hatch date and the median hatch date of the corresponding season, by the standard deviation of the hatch date for the same season. Because nestlings reared at the same nest were not independent from each other the identity of the nest of development was included as a random effect. The identity of the nest of origin was also tested as a random effect but it was removed from the final model because it

was not significant. Its addition as a second random effect increased the AIC value of the model and, when the reduced model, with only nest of development as a random term was compared against the model with both random terms, a p-value of 0.19 was obtained. The general model included three fixed effects, and two-way interactions; stepwise-deletions were used to investigate the effects of these explanatory terms (Crawley 2007). Non-significant interactions and terms were removed one by one according to descending order and p-values. Markov chain Monte Carlo (MCMC) simulations were used to estimate p-values and confidence intervals for the fixed parameters (Baayen et al. 2008) fitted using the function lmer from the free program R ver. 2.11.1. Male and female mass were compared using ANOVA, while nestling period, fledging success, number of nestlings fledged, and return rates were analyzed using non-parametric tests. ANOVAS and non-parametric tests were performed in Statistica ver. 7.

## Results

No statistical difference in hatchlings' mass was found among the 35 triads (105 nests) used to form the experimental groups (Kruskal–Wallis;  $n = 104$  nests,  $H = 0.7$ ,  $p = 0.7$ ).

### Parental effort

At day 4, males' feeding rate was higher at enlarged than at control and reduced broods (Kruskal–Wallis;  $n = 87$ ,  $H = 23$ ,  $p < 0.001$ , a posteriori contrasts; Fig. 1A). Females' feeding rate was higher at enlarged broods than at reduced ones, but no other differences were found (Kruskal–Wallis;  $n = 87$ ,  $H = 12.9$ ,  $p = 0.002$ , a posteriori contrasts; Fig. 1A). At day 12, both feeding rates of males and females at enlarged and control broods were similar and higher than feeding rates at reduced broods (a posteriori contrasts, Kruskal–Wallis; males:  $n = 76$ ,  $H = 15.4$ ,  $p < 0.001$ ; females:  $n = 76$ ,  $H = 18.1$ ,  $p < 0.001$ ; Fig. 1B).

Per nestling feeding rate of both males and females when nestlings were four days old were similar at control and enlarged broods and higher at reduced broods (females rank: 4.9–2.6 feedings/H and N; males rank: 2.4–1.5 feeding/H and N; Kruskal–Wallis;  $n = 87$ , females:  $H = 50.5$ ,  $p = 0.001$ ; males:  $H = 6.5$ ,  $p = 0.04$ , a posteriori contrasts). When nestlings were 12 d old, per nestling feeding rate of males was similar at all treatments (rank: 2.6–2.1 feeding/H and N; Kruskal–Wallis;  $n = 76$ ,  $H = 1.1$ ,  $p = 0.6$ , a posteriori contrasts). Females, however, visited the nests at a similar rate per nestling and hour at reduced and control broods, and diminished it at enlarged broods (rank: 4–2.3 feeding/H and N; Kruskal–Wallis;  $n = 76$ ,  $H = 12.3$ ,  $p = 0.002$ , a posteriori contrasts).

We do not consider these treatment differences were due to different weather conditions because: 1) we did not record feeding behaviors on rainy days or with bad weather conditions resulting on similar and relatively good weather conditions during all recordings; and 2) each day we recorded feeding visits on several nests belonging to the different treatments.

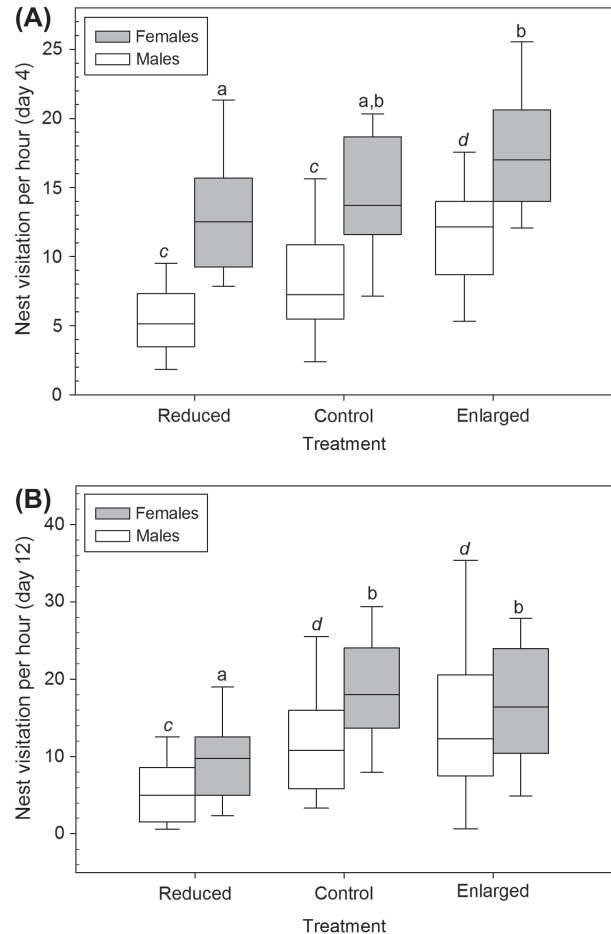


Figure 1. Parental investment of *Tachycineta leucorhoa* (males and females) in three experimental groups (reduced broods:  $-2$ ; control broods:  $0$  and enlarged broods:  $+2$ ). Nest visitation rates per hour when nestlings were four (A) and (B) 12 d old for males and females. Letters denote statistical differences ( $p < 0.05$ ) within sexes and between treatments, median and 25% percentiles are shown.

### Nestlings' development and return

In line with the observed nest-feeding rate, similar nestlings' development rates were found when nestlings' mass was adjusted to an independent logistic growth curve for each treatment. The growth rate ( $k$ ) of nestlings was 0.36, 0.35 and 0.38 for enlarged; control, and reduced broods, respectively (Fig. 2). Likewise, nestling periods of enlarged and control broods were equal ( $M = 24$  d) and significantly longer than the nestling period found at reduced broods ( $M = 23$  d; Kruskal–Wallis;  $n = 72$ ,  $H = 9.8$ ,  $p = 0.007$ , a posteriori contrasts). Nestlings at fifteen days old in enlarged broods were as heavy as nestlings raised in control broods, but lighter than nestlings raised in reduced broods of the same age (Table 1). The standardized hatch date and the year were not related to nestlings' mass.

No differences in fledging success were found among treatments (Kruskal–Wallis;  $n = 105$  nests,  $H = 5.3$ ,  $p = 0.07$ ) but, as expected, the number of fledglings was different (Kruskal–Wallis;  $n = 105$  nests,  $H = 9.9$ ,  $p = 0.007$ ;

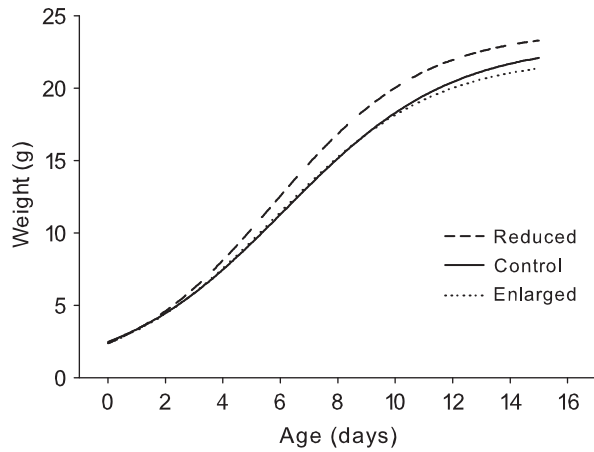


Figure 2. Logistic growth curves of nestlings at control, reduced and enlarged broods. The estimated asymptotic mass was 23.97 g, 23.14 g and 22.14 g for reduced, control and enlarged groups respectively.

M = 6, 4 and 2 nestlings at enlarged, control and reduced broods, respectively). These results together reflected the brood size manipulation and the ability of white-rumped swallows to cope with the challenge of an increased brood size. After comparing the percentage of nests that failed completely without signs of predation, enlarged broods failed significantly more often than control and reduced broods: 40%, 26% and 23%, respectively (Fisher's exact test; enlarged vs control:  $p = 0.03$ ; enlarged vs reduced:  $p = 0.008$ ). In a reduced sample size we were able to estimate adults' age based on number of captures (i.e. individuals with at least three years old): we determined the age of 43% of the adults raising failed broods and 45% of the adults that raised a successful brood. The mean age of failed females was  $1.8 \pm 0.4$  yr and  $3.3 \pm 1.1$  yr for successful ones (differences between means:  $N_f = 7$ ,  $N_s = 12$ ;  $p = 0.005$ ); and the mean age of males raising failed and successful nests did not differ significantly (failed:  $1.8 \pm 0.8$  yr,  $N_f = 5$ , successful:  $2.6 \pm 1.1$  yr,  $N_s = 7$ ;  $p = 0.2$ ).

Only eight of 254 nestlings that fledged from experimental nests were recaptured as breeding adults, a return rate of 3% that precluded any statistical analysis given the small sample size (four, one and two birds raised at enlarged, control, and reduced broods, respectively).

Table 1. Generalized linear mixed model analysis: fixed and random factors affecting nestlings' mass at 15 d of age after a brood size manipulation. The minimum model is shown after removing all the non significant effects.

	Estimate	Error	p-value (MCMC)
<b>Fixed effects</b>			
intercept	21.99	0.36	0.001
reduced	1.53	0.52	0.0006
enlarged	-0.42	0.53	0.2056
	Variance	CI 95% lower	CI 95% upper
<b>Random effects</b>			
nest ID	2.82	0.78	1.18
residual	2.03	1.54	1.86

## Adults' condition and survival

No differences among treatments were found in females' mass variation between our measure during the incubation period and day 9–10 of the nestling period (ANOVA; females:  $n = 79$ ,  $F = 0.5$ ,  $p = 0.6$ ). We found no difference in males' mass after having fed broods of different sizes (ANOVA; males:  $n = 80$ ,  $F = 0.4$ ,  $p = 0.65$ ). The same results were obtained when the body condition index for each sex was compared among treatments (ANOVA; females:  $n = 76$ ,  $F = 0.8$ ,  $p = 0.4$ ; males:  $n = 80$ ,  $F = 0.8$ ,  $p = 0.45$ ).

Combined apparent return rates of the adults were 36.6 % for males and 48.6 % for females ( $N_{t0} = 82$  and 105 individuals;  $N_{t+1} = 30$  and 51 respectively). Return rates of females that had raised enlarged or reduced broods during the previous season were not statistically different from females raising control broods (Fisher's exact test,  $p_{\text{enlarged vs control}} = 0.06$  and  $p_{\text{reduced vs control}} = 0.09$ , Table 2). The return rate of males was also not affected by the brood size manipulation (Fisher's exact test,  $p_{\text{enlarged vs control}} = 0.54$  and  $p_{\text{reduced vs control}} = 0.19$ , Table 2).

Finally, costs that potentially could influence the future reproductive success of adults were evaluated among treatments. The laying date, clutch size, hatching and fledging success of adults one season after having their brood size manipulated (enlarged or reduced) were not different from the breeding parameters of those adults that had raised control broods (all  $p > 0.6$  for males and females, Table 3).

## Discussion

The most recent studies using brood size manipulations as a tool to investigate different aspects of the reproductive biology of bird species have been conducted in the north temperate region (Saino et al. 2003, Bañura et al. 2008, Hainstock et al. 2010, Arnold 2011). A smaller number of similar studies conducted across tropical environments have also been published in the past decades (Beissinger 1990, Young 1996, Stoleson and Beissinger 1997, but see Styrsky et al. 2005). Similarly, there are several studies with experimental brood size manipulations in a north temperate congener, the tree swallow (De Steven 1980, Wiggins 1990, Wheelwright et al. 1991, Murphy et al. 2000, Shutler et al. 2006) but, to our knowledge, this is the first study in which this experimental design is used to understand the life history strategy of a southern South American species.

Table 2. Number of adults that returned to breed to Chascomús after being exposed to the different treatments and the percentage that returned based on the initial number of adults captured within each experimental group (93 females and 70 males).

	Females		Males	
	n	Return %	n	Return %
Reduced	15	42.9	8	22.9
Control	22	62.9	11	39.3
Enlarged	14	40	11	31.4

Table 3. Breeding performance of white-rumped swallows one season after the brood size manipulation ( $t+1$ ). Values represent the mean  $\pm$  SE for reduced, enlarged and control broods. p-values from Kruskal–Wallis are reported for clutch size, hatching success and fledging success, and from ANOVA for lay date (standardize laying date). Due to nest failure hatching and fledging success samples size decreased, and data from 2010 breeding season for lay date was not included ( $n = 5$  females, 3 males).

	Reduced	Control	Enlarged	p	n
Clutch size					
female	5.13 $\pm$ 0.35	5.00 $\pm$ 0.31	5.07 $\pm$ 0.62	0.63	51
male	5.13 $\pm$ 0.35	5.18 $\pm$ 0.40	5.18 $\pm$ 0.60	0.94	30
Hatching success					
female	0.92 $\pm$ 0.10	0.91 $\pm$ 0.15	0.77 $\pm$ 0.38	0.74	49
male	0.93 $\pm$ 0.15	0.89 $\pm$ 0.14	0.89 $\pm$ 0.14	0.71	30
Fledging success					
female	0.82 $\pm$ 0.33	0.85 $\pm$ 0.36	0.90 $\pm$ 0.30	0.98	47
male	0.81 $\pm$ 0.37	0.83 $\pm$ 0.31	0.91 $\pm$ 0.30	0.68	30
Lay date					
female	-0.29 $\pm$ 0.09	-0.18 $\pm$ 0.09	-0.22 $\pm$ 0.12	0.80	46
male	-0.17 $\pm$ 0.19	-0.19 $\pm$ 0.08	-0.11 $\pm$ 0.16	0.90	27

### Current reproductive decisions: parental effort and nestling development

When nestlings were four days old, males and females increased the feeding rate at enlarged nests (in the case of females the increase did not reach statistical significance), suggesting they responded to the higher need of an enlarged brood. During day 12, feeding rates of males and females were similar between enlarged and control broods, but diminished at reduced broods, this time suggesting a reaction to nestling satiation. We did not estimate size of food loads during feeding visits, so we cannot eliminate this as a potential contributor on parental effort. However, this assumption has been tested in similar species where males and females provided similar amounts and types of food (Quinney 1986, McCarty and Winkler 1999, McCarty 2002), and brood size did not influence size of food loads (McCarty 2002). It is also interesting to note that the maximum feeding rate observed (at both stages of development and along all treatments) was very similar to the value reported in a previous study in the same species and site but where brood sizes were not manipulated (Bulit et al. 2008): 18.7 females' visits per hour (present study) and 18.6 visits per hour (previous study). These results suggest two scenarios: 1) white-rumped swallows were able and willing to make an adjustment of the feeding visits in response to an increase in the current cost of reproduction as was found in several species (reviewed by Dijkstra et al. 1990, Stearns 1992); and 2) there seems to be an upper limit to the number of feeding visits on this species. This kind of limit has been also stated for tree swallows (Murphy et al. 2000): similar rates between broods of seven, eight and nine nestlings. The parental effort made by white-rumped swallows with enlarged broods was also evidenced by nestlings' growth rates and mass: growth rates of nestlings from enlarged and control nests were almost equal, and the mass of 15-d- old nestlings was the same in enlarged and control nests, in line with the conclusion that adults managed to feed enlarged broods. The per-nestling feeding rates were also consistent as they were similar at enlarged and control broods when nestlings were 4 and 12 d old. These results are contrary to

all previous studies conducted in tree swallows in which nestlings' mass at enlarged broods decreased when compared to control broods (Wiggins 1990, Wheelwright et al. 1991, Burness et al. 2000, Murphy et al. 2000; for the same tendency, but not significant results see De Steven 1980). The resulting nestling period of white-rumped swallows confirmed that nestlings raised at enlarged nests were not at a disadvantage in spite of the fact that the adults were raising more nestlings than they would originally have.

Fledging success, i.e. the proportion of hatchlings that fledged, was similar among treatments and white-rumped swallows raised more nestlings at enlarged than at control and reduced nests, respectively. The productivity of nests, therefore, increased with the total number of young present at the nests, similarly to the results found in all tree swallow studies (Murphy et al. 2000, Shutler et al. 2006). This result also supports previous ones: adults were able to cope with an enlarged brood. However, total nesting failure without signs of predation was more common at enlarged broods, a result not reported in tree swallow studies. Higher nestling mortality in enlarged broods suggests that this treatment increased the costs of reproduction and could also be interpreted as a proof of the phenotypic plasticity of the adults' behavioral response as some individuals were not able or willing to bear the augmented costs, and transferred the costs to the young.

Most individuals included in this experiment were of unknown age as this species does not show female age-related plumage differences as other swallows do (Hussell 1983, Bitton et al. 2007). However, using capture-based age estimations and after comparing the minimum age of recaptured adults, failed nests more often belonged to yearling females. Young individuals are less experienced and poorer breeders, usually laying smaller clutch sizes and raising fewer young (Stutchbury and Robertson 1988, Ardia and Clotfelter 2007). The poor performance of youngsters may stem from different causes: they may lack the needed experience and are unable to perform well (Nielsen and Drachmann 2003, Riechert et al. 2012), or young individuals may not be willing to compromise the prospect of future reproductions (Williams 1966, Ardia 2005). When

confronted to a reproductive challenge, older individuals would theoretically be more willing to risk the prospect of future reproduction, investing more in the current brood than younger individuals, thus contributing to the phenotypic plasticity found in response to the reproductive challenge presented to them (Williams 1966, Velando et al. 2006, but see Warner et al. 2013).

### Residual reproductive value: adults' condition and survival

The reduction in females' mass between incubation and the rearing period was similar among treatments; males' mass after having fed enlarged, control and reduced broods during eight days was also similar. No differences in the body condition indices of males and females among treatments were found either. These results indicate that adults did not experience a measurable cost in any of these variables in accordance with the results obtained in tree swallow manipulations (Murphy et al. 2000, Shutler et al. 2006). The absence of costs measured in mass or body condition does not, however, preclude the existence of other short- or long-term reproductive costs, such as a potential impact on the immune function (Ardia et al. 2003) not measured in this study. In the present study we did not detect a short-term effect on adults' condition.

We found no difference in the return rate of males and females exposed to different treatments, as was also described in the case of tree swallows (Murphy et al. 2000, Shutler et al. 2006). In a previous study we found that successful females were more likely to return than unsuccessful ones (Bulit and Massoni 2011), a frequent pattern described for birds (Greenwood and Harvey 1982, Clark and Shutler 1999, Winkler et al. 2004, but see Shutler and Clark 2003). Given that a greater percentage of enlarged nests failed completely, we expected to find smaller return rates in females that had raised those broods; instead, the return rate was similar to that of females who raised reduced broods. This suggests white-rumped swallows females may be sensitive not only to complete nest failure (Bulit and Massoni 2011), but also to a discrepancy between their individual clutch size and the brood size they were forced to raise by manipulating their brood (Pettifor et al. 1988, 2001). Males' return rate was unaffected by treatments, as was earlier determined for both species (Shutler et al. 2006, Bulit and Massoni 2011). Even though return rates do not accurately reflect adult survival, the returns rates found on this study agree with previous return rates described for this species in the same field-site: 43.5% for females (59% for successful females) and 42% for males (Bulit and Massoni 2011). The reduced sample size of the present study did not allow us to estimate apparent survival based on model selection procedures and capture-recapture data. As we cannot rule out dispersal or permanent emigration, we can interpret return rates only as an indicator of adult survival.

Our data did not support a reduced reproductive effort of white-rumped swallows one year after the enlarged treatment, again consistent with tree swallow studies (Wheelwright et al. 1991, Shutler et al. 2006). The breeding parameters of those adults who raised experimental

broods and returned to breed at Chascomús were not affected by the treatment, suggesting the costs borne by the adults were not large enough to produce long term effects over the following season and that those individuals could be of higher intrinsic quality than the ones who failed to raise the enlarged broods.

### Life history strategy

We expected a fast living species would increase effort with brood size and produce good quality offspring independently of the brood size, accepting the costs of greater reproduction reflected on a reduced adult body mass or condition, return rate or future reproductive parameters.

The majority of the results found after manipulating the brood size of the white-rumped swallow are consistent with those obtained with the fast living tree swallow. The main difference found is that most white-rumped swallows fed the enlarged broods at a rate that produced offspring that grew and fledged as if they belonged to control nests, emphasizing this swallow did not curtail efforts to raise their current brood. As is also the case in tree swallows (De Steven 1980, Murphy et al. 2000), we did not detect measurable costs of raising enlarged broods in terms of mass loss or reduced body condition. Costs of reproduction on the long-term immune function have been found in that species (Ardia et al. 2003); if white-rumped swallows were making a comparable or even larger parental effort than tree swallows, as evidenced by their higher per capita feeding visit, we would expect to find their long-term immune system compromised. We did not detect reduced return rates for individuals raising augmented broods, neither an increase, as reported for tree swallows (Murphy et al. 2000; but see Shutler et al. 2006). We caution, however, that we were unable to measure long term survival, and that not returning to breed not necessarily implies an individual is dead.

White-rumped swallows have a clutch size about one egg smaller than do tree swallows (Zach 1982, Ramstack et al. 1998, Murphy et al. 2000), similar incubation period, and a slightly slower growth rate and longer nestling period (Massoni et al. 2007). They also have a higher frequency of feeding visits, suggesting a larger cost of reproduction, and survival rates that are closer to the lowest values reported for tree swallows (Bulit and Massoni 2011). This information, and the fact that most swallows at enlarged nests were successful at raising well-fed nestlings until they fledged, suggests this species should be indeed considered as having a fast pace life history strategy, resembling north temperate swallows (*T. bicolor* and *T. thalassina*). Four recent studies have reconstructed phylogenetic hypotheses for the *Tachycineta* genus based on nuclear or mitochondrial DNA (Whittingham et al. 2002, Sheldon et al. 2005, Cerasale et al. 2012, Dor et al. 2012). All of them support a South and Central American clade ((*T. leucorrhoa*, *T. meyeri*), (*T. stotzmanni*, *T. albiventer*, *T. albilinea*)) but disagree on the structure and position of the North American and Caribbean clade ((*T. bicolor*, *T. thalassina*), (*T. cyaneovirdis*, *T. euchrysea*)). Despite the different hypotheses proposed for Caribbean species, the most relevant discrepancy in light of the present study is

the location of *T. bicolor*. Based on mtDNA *T. bicolor* is situated in a clade including North American and Caribbean species (Whittingham et al. 2002, Sheldon et al. 2005, Cerasale et al. 2012) and based on bayesian nDNA reconstructions it is considered as a sister species to all other *Tachycineta* (Dor et al. 2012). Based on a mitochondrial phylogenetic framework and genetic distances *T. leucorrhoa* life history should be similar to the sister species *T. meyeni* or closely related species as the rest of the South and Central American clade (Whittingham et al. 2002). Our results however do not support this pattern, and in contrast are in line with a geographic variation of life history strategies along a latitudinal gradient (Supplementary material Appendix 1, Table A1, but see Liljeström et al. 2012a, b).

We are certain this kind of experimental approach should be conducted more often in South America (Sousa and Marini 2012), especially in the southern region of South America. As was clearly stated, the amount of information on north temperate species is very large in comparison to tropical and southern temperate species (Martin 2004). In particular, the important and undeniable progress attained by comparative studies including southern South American birds stem from a study site placed only 4 degrees away from the Tropic of Capricorn (Ghalambor and Martin 2001, Martin et al. 2006, Chalfoun and Martin 2007). We believe the patterns found in the life history traits and tradeoffs in those studies are representative of an important number of tropical and subtropical species and are applicable to climatic and ecologically similar areas in this continent, but the wealth of subtropical or more southern South American species' life history traits and strategies remains relatively unknown. It is important to define if the paradigms and, even more important, the conclusions based on north temperate vs tropical and subtropical species are adequate to describe south temperate species of the western hemisphere (Moreno 2004, Moreno et al. 2005). Until a larger number of species that inhabit southern regions are studied, the pattern of life-history strategies of southern South American birds will remain partially understood. We encourage researchers to include more species from southern latitudes like the one described here to increase our knowledge about life history variations in a broader context. This study is based on one species and did not include data comparisons among species in a broader geographical range, however we are convinced about the importance of incorporating species of more southern latitudes in building conclusions around life history theory and living strategies.

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Supplementary material (Appendix JAV-00266 at <[www.oikosoffice.lu.se/appendix](http://www.oikosoffice.lu.se/appendix)>). Appendix 1.