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# Weather conditions, brood size and hatching order affect Common Swift *Apus apus* nestlings' survival and growth

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**Capsule** Hatching order negatively affected Common Swift *Apus apus* nestlings' survival, while brood size and meteorological conditions influenced their growth patterns.

**Aims** To investigate the influence of hatching date, age, sex, brood size and meteorological conditions on survival and growth of Common Swift nestlings from Northern Italy (Southern Europe), a relatively warm and dry part of the distribution range of this species.

**Methods** Nestlings were weighed at regular intervals and molecularly sexed. Growth patterns were described using a double-Richards growth curve, i.e. a growth curve that also accounted for the pre-fledging mass loss. We also identified the Linear Growth Phase (i.e. when nestlings grew at the fastest rate).

**Results** Mortality increased with hatching order and decreased with brood size. Mortality was highest for fourth-hatched nestlings, none of which survived. Nestlings hatched late in the season grew faster, experienced the fastest growth rate at a younger age, but reached a lower maximum weight than nestlings hatched early in the season. Nestlings from large broods reached a lower maximum weight than those of small ones. Nestlings gained more mass when temperature was slightly higher than that expected from the seasonal temperature trend, and on rainy and windy days.

**Conclusion** Common Swift nestlings' growth, but not survival, was affected by meteorological conditions, with moderate rainfall, moderate winds and high temperatures favouring greater mass gain. Higher intra-brood competition resulted in slower growth and lower maximum weight. Late-hatched nestlings grew faster but reached a lower maximum weight and a lower pre-fledging mass, possibly suggesting that late-hatched nestlings adaptively tune their growth pattern to the approaching onset of migration to their African wintering quarters. Our results emphasize the importance of exploring weather effects on the breeding biology of a species in different portions of its distribution range that are characterized by contrasting climatic conditions.

The environmental conditions experienced by an organism during ontogeny may have important long-term consequences on several traits of its life history (review in Burness *et al.* 2000). Variation in the quality of the rearing environment can result in differences in the physiological condition (Burness *et al.* 2000) or in the morphology of offspring (Boag 1987, de Kogel 1997) and in differences in their survival prospects during the early phases of life (Dijkstra *et al.* 1990, Hall *et al.* 2001), but can also have long-lasting, organizational effects,

affecting adult physiology or morphology (Perrins 1965, Haywood & Perrins 1992, Schluter & Gustafsson 1993, de Kogel & Prijs 1996). In birds, individuals raised under poor conditions often reach a smaller size, lighter body mass at fledging and have lower overwinter survival and recruitment than those raised in a more favourable environment (Perrins 1965, Boag 1987, Richner 1989, Dijkstra *et al.* 1990, Koskela 1998). In adult life, these individuals may breed in low-quality habitats (Verhulst *et al.* 1997), have lower fecundity (e.g. smaller clutch sizes; Haywood & Perrins 1992, Schluter & Gustafsson 1993) or reduced attractiveness

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with respect to conspecifics (Gustafsson *et al.* 1995, de Kogel & Prijs 1996). Therefore, the environment where an individual is reared may have crucial effects on its subsequent behaviour (Rosenzweig 1984), viability and fitness (Lindström 1999, Saino *et al.* 2012).

The rearing environment of an individual is determined by both abiotic and biotic factors, which can also vary at different spatial and temporal scales. For instance, among abiotic factors, meteorological conditions greatly affect nestlings growth in many bird species (Roldan *et al.* 2013, Chausson *et al.* 2014), because they impact on individuals both directly, e.g. by affecting thermoregulation costs and energy expenditure of nestlings (Ricklefs 1983), and indirectly, by influencing food availability or the foraging efficiency of parents, for example. Direct negative effects of temperature on growth could result either from raised energetic needs due to increased costs of thermoregulation under cold conditions or from the increase in the costs of dissipating heat when exposed to hot conditions (Speakman & Krol 2010).

Other factors may, however, have an equally important role in influencing the pre-fledging survival and growth. For example, the number of siblings in each brood can affect the intensity of sib-sib competition, resulting in a lower per capita food provisioning. In addition, in species where hatching asynchrony determines a hierarchy among nestlings, hatching order may affect the ability of nestlings to compete with nest mates for resources. Many studies also suggest that male and female offspring may differ in their ability to compete for food (Teather 1992), and may be differentially affected by environmental conditions (Kalmbach *et al.* 2005). Such differences have also been observed in species that are strictly monomorphic like the Alpine Swift *Thakymarptis melba* (Bize *et al.* 2005). Sex differences in competitive abilities may be exacerbated when rearing conditions deteriorate (Kalmbach & Benito 2007, Saino *et al.* 2008, Jones *et al.* 2009, Rosivall *et al.* 2010). For instance, in the Blue Tit *Cyanistes caeruleus*, female nestlings are more sensitive to adverse environmental conditions in terms of reduced fledgling size than their brothers (Råberg *et al.* 2005), while the contrary held true in the Barn Swallow *Hirundo rustica* (Boncoraglio *et al.* 2007).

Here we investigated the influence of the rearing environment on Common Swift *Apus apus* nestlings' survival and growth in a colony in Northern Italy. The Common Swift is a medium-sized, long-lived species which lays only one clutch of two to three eggs per year, with a laying interval of two to three days, while clutches of one or four eggs are less frequent (Cramp

1998). Incubation lasts 20–22 days and eggs typically hatch asynchronously with a delay of 24 hours between each egg. Nestlings are fed by both parents until fledging. No post-fledging parental care is known in this species (Cramp 1998).

Previous studies (Lack 1956, Perrins 1964) have indicated that mortality in this species is very high before fledging and that growth patterns profoundly affect long-term fitness, because a higher body mass at fledging and a delay in the time of fledging can increase survival probability (Perrins 1965, 1988). Nestling mortality is mainly due to starvation (Lack 1956, O'Connor 1979), which, in turn, is related to inclement weather conditions (Lack & Lack 1951, Gory 1987, Cucco *et al.* 1992, Thomson *et al.* 1996). Being aerial feeders, Common Swifts are particularly sensitive to meteorological conditions because both their foraging success and the availability of invertebrate prey can be severely affected by adverse weather (Avery & Krebs 1984, Arlettaz *et al.* 2010). Indeed, adults can prolong incubation during periods of bad weather (Cramp 1998), and age at fledging strongly depends on weather conditions (Hudec 1983). Brood size and nestling features can also affect survival and growth patterns by modulating the intensity of intra-brood competition for resources. Despite the fact that the Common Swift is a monomorphic species, males and female nestlings may show different susceptibility to rearing conditions, as demonstrated in the closely related Alpine Swift (Bize *et al.* 2005), or differ in their ability to compete with nest mates for resources.

Furthermore, the reproductive period in the Common Swift is tightly scheduled. Adults start nesting soon after their arrival at the breeding quarters and leave soon after fledging of their nestlings or even a few days before (Cramp 1998). Timing of breeding may therefore influence offspring survival, because nestlings born late in the season may suffer higher mortality due e.g. to premature nest desertion by parents (especially by inexperienced individuals at their first breeding attempt; Cramp 1998).

Because many offspring developmental traits can potentially be affected by their rearing environment, we took into account different aspects of nestlings' early stages of life. First, we investigated the influence of meteorological conditions, brood size, hatching date, position in the hatching hierarchy and age, on nestling survival. Secondly, we analysed variation in nestlings' growth patterns from hatching to fledging according to brood size, hatching date, sex and hatching order. Throughout, we refer to 'growth' as the overall gain in mass of individuals, including thus both skeletal and

muscle growth (and accumulation of fat towards the pre-fledging period). In order to analyse growth patterns, we interpolated growth curves from repeated measures of nestlings' body mass to fully describe the growth trajectory of each nestling. We were interested in investigating potential differences in the entire pattern of nestling growth because the entire growth trajectory, and not just the final mass nestlings achieved, may affect their future survival (Gebhardt-Heinrich & Richner 1998). Because Common Swift nestlings experience a period of considerable body mass recession (up to 20% of their weight) before fledging, we used double-Richards (or positive-negative Richards) growth curves, which are able to fully describe both nestlings growth and their following mass recession (Oswald *et al.* 2012). Thirdly and finally, we investigated the possible effects of weather conditions on nestling growth rate and their potentially differential influence on nestlings of different sex, age and hatching order. In particular, we focused on the linear phase of nestling growth (hereafter Linear Growth Phase (LGP)) because during this phase nestlings grow at maximum rate and are expected to be maximally sensitive to short-time variation in meteorological conditions (Lack 1956).

Overall, based on previous studies, we expected mortality to increase during spells of bad weather (Lack & Lack 1951, Rajchard *et al.* 2006), and in large clutches, where the negative effects of the hatching hierarchy should be more evident. In addition, we expected nestlings to grow faster in smaller broods (Martins 1997) and, among broods, to observe a large difference between the first and last hatched sibling (Martins 1997), with the latter showing slower growth as a result of its disadvantage in the hierarchy among siblings for access to parentally delivered food. We also expected growth rates during the Linear Growth Phase to decrease during bad weather conditions. Finally, we had no clear predictions concerning sex differences in growth and environmental susceptibility because sex differences have not been taken into account in previous studies of Common nor of the closely related Pallid Swift *Apus pallidus* (Martins & Wright 1993, Cucco & Malacarne 1996, Martins 1997). However, according to previous studies on Alpine Swifts, we might expect that female nestlings are more susceptible to harsh rearing conditions (Bize *et al.* 2005).

## METHODS

### Study site and data collection

Fieldwork was carried out from 20 April to 2 August 2012 in a colony breeding in a tower in San Paolo,

Brescia, Italy (45°22'10.57" N, 10°01'34.01" E). The tower hosts 284 artificial cavities used by Common Swifts for nesting, which can be easily accessed from inside the tower.

Nests were inspected every two to four days to assess hatching date and monitor nestling growth. When a nestling was found for the first time its hatching date (and hence hatching order) was determined according to its morphological features (Jongsomjit *et al.* 2007, Tigges 2008). The mean value of hatching order was used for nestlings for which a clear size hierarchy was not evident and thus likely hatched on the same day (for example, 1.5 is the hatching order of the first two siblings hatched on the same day). All newly hatched nestlings were marked with different non-toxic colours on the skin of the legs in order to be individually identified until they reached an age when they could be ringed (10–12 days) with individual metal rings.

At each visit, nestlings were weighed to the nearest 0.1 g by means of a digital balance (Constant Digital Pocket Scale 14192-97, US Balance, Vincennes, IN). At ten days of age we collected a blood sample for molecular sexing from each nestling by puncturing the brachial vein. Blood was collected in heparinized capillary tubes and stored fresh while in the field and then frozen at  $-20^{\circ}\text{C}$  within a few hours from collection.

### Molecular sexing

Nestlings were sexed after PCR amplification of the sex-specific avian CHD gene. DNA extraction was performed by an alkaline lysis of blood samples with 50 mM NaOH. Between 50 and 100 ng of genomic DNA was used as template. A region of the CHD gene was amplified using the P2 and P8 primers proposed by Griffiths *et al.* (1998). The amplification was carried out in a total volume of 15  $\mu\text{l}$  with the following final reaction conditions: 2 mM  $\text{MgCl}_2$ , 0.2 mM of each deoxynucleotide (dNTPS) (Fermentas, Vilnius, Lithuania), 100 ng of each primer (Sigma-Genosys, St. Louis, MO), 0.625 units of Taq polymerase (Promega, Waltham, MA) and 5X Green GoTaq Flexi Buffer. Polymerase chain reaction was carried out in a T1 thermocycler (Biometra, Goettingen, Germany) under the following conditions: 94  $^{\circ}\text{C}$  for 7 minutes, followed by 30 cycles of 48  $^{\circ}\text{C}$  for 30 seconds, 72  $^{\circ}\text{C}$  for 30 seconds and 94  $^{\circ}\text{C}$  for 60 seconds. The reaction finished with the last steps of 48  $^{\circ}\text{C}$  for 30 seconds and 72  $^{\circ}\text{C}$  for 5 minutes.

155 PCR products (15  $\mu$ l) were digested with Hae III and  
 Asp700I (Roche Diagnostics, Mannheim, Germany),  
 following the procedures described in detail in Sacchi  
*et al.* (2004). We stress that the combined use of the  
 two enzymes should avoid any misleading assignment.  
 160 AQ4 Digestion products were analysed by agarose gel  
 electrophoresis (2% in Tris borate EDTA) and  
 visualized under UV light after ethidium bromide  
 staining. GeneRuler 50 bp DNA Ladder (Fermentas,  
 Vilnius, Lithuania) was used as size marker. A single  
 band identified a male and two different bands  
 165 identified a female.

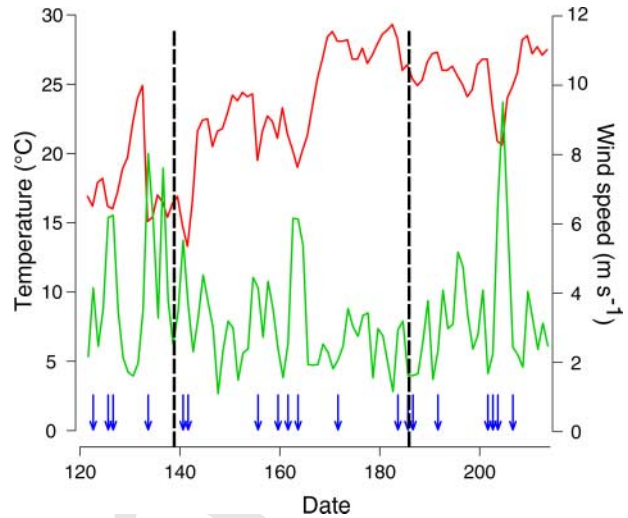
Positive controls obtained from adults of known sex  
 were included in the sexing protocol.

### 170 Meteorological variables

175 Data on air temperature measured 60 m above ground  
 level, and rainfall collected at one-hour intervals at a  
 meteorological station located about 9 km from the  
 colony were obtained from the Agenzia Regionale  
 per la Protezione dell'Ambiente (ARPA, [www.  
 arpalombardia.it](http://www.arpalombardia.it)). Data on wind speed were obtained  
 from the Reanalysis I Project of the National Oceanic  
 and Atmospheric Administration ([http://www.cdc.  
 noaa.gov](http://www.cdc.noaa.gov)). We use the *NCEP.interp* procedure of the  
 RNCEP package in R (Kalnay *et al.* 1996) to  
 180 interpolate the mean value of both U- (East/West,  
 variable 'uwnd') and V-Wind Component (North/  
 South, variable 'vwnd') at one-hour intervals from the  
 1000 mb to the 925 mb pressure level (approximately  
 from ground level up to 750 m from ground). We then  
 185 calculated for each hour the total wind speed as the  
 square root of the sum of the squared values of U-  
 Wind and V-Wind. Finally we calculated mean  
 daily values of wind speed. Throughout the paper dates  
 are expressed as days from 1 January = 1 (Fig. 1).

### Mortality analyses

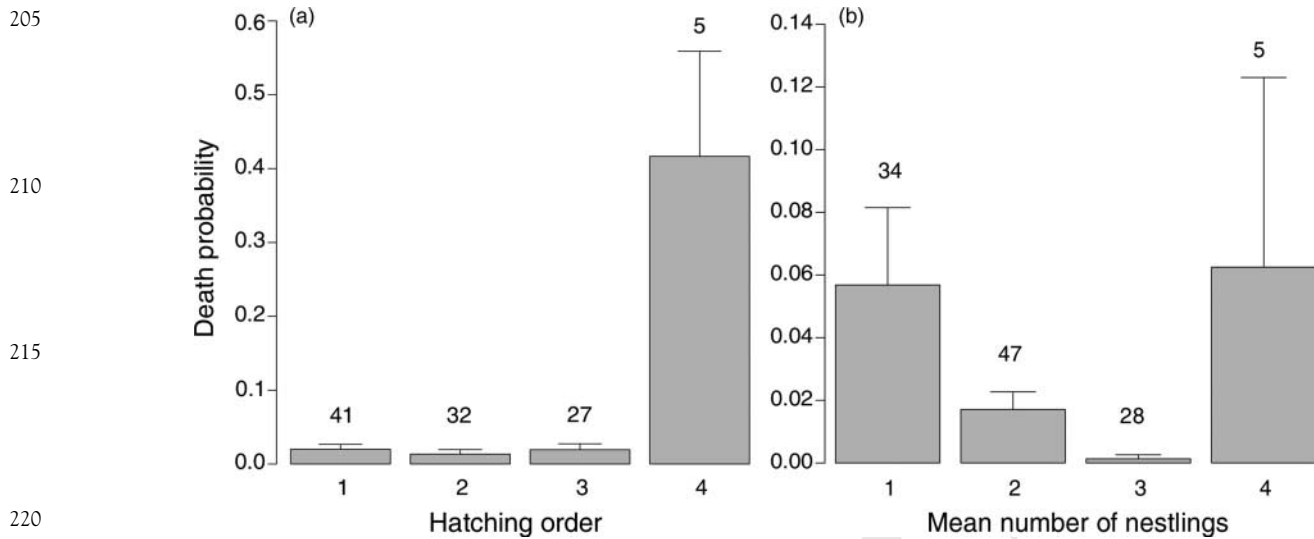
195 Individual mortality was assessed at each visit by recording  
 all nestlings found dead in the nest. In addition, all nestlings  
 that disappeared from the nest before the age of 35 days  
 were considered dead because this is the minimum age  
 recorded at fledging (Cramp 1998). For each nestling we  
 200 generated a dichotomous variable ('death') indicating  
 whether it died (or disappeared prematurely; death = 1)  
 in the days between consecutive visits at the nest (simply  
 'interval' hereafter), or it was present at the nest during  
 an interval (death = 0). We calculated the mean number



**Figure 1.** Meteorological conditions during the entire study period in the study area in Northern Italy. In red: mean daily values of temperature; in green: mean daily values of wind speed; blue arrows indicate days when rainfall events occurred. Rainfall events varied between a total of 0.2 and 44.0 mm rain per day. Dashed lines delimit the period that includes the Linear Growth Phase for all nestlings of the colony. Dates are expressed as days from 1 January = 1.

of nestlings in the nest during each interval as the mean number of nestlings found in consecutive visits at the nest. This variable should account for the intensity of sibling competition for parental resources during each interval. We also calculated the mean age of each nestling during each interval. Mean date and mean nestling age at each interval were highly correlated ( $r = 0.79$ ). In order to account for potential seasonal effects, we therefore included nestling age and hatching date instead of mean date of each interval among predictors. Mean temperature at each interval and nestling age were highly correlated ( $r = 0.66$ ). We therefore calculated the residuals from the regression of mean temperatures on mean dates and included this variable as covariate in the model because it was not correlated with age ( $r = 0.11$ ). Hence, negative values of temperature residuals indicate lower temperatures than those expected from the seasonal trend, and positive residuals higher temperatures. Temperature residuals were negatively correlated with rainfall ( $r = -0.44$ ) and with wind speed ( $r = -0.62$ ), while the correlation between rainfall and wind speed was weak ( $r = 0.21$ ).

To properly model death events, we built a discrete time hazard model (because death events were assessed only during visits at a nest) that also included random effects to account for repeated observations of the same nestling (up to its death or its fledging) and for clustering of nestlings within broods. This type of model can be built



**Figure 2.** Mortality in relation to: (a) hatching order and (b) mean number of nestlings present in the nest. Bars represent binomial standard errors and numbers represent number of nestlings in A and number of nests in B. Only integer values of mean number of hatching order and nestlings are shown.

using a Generalized Linear Mixed Model (GLMM) assuming a binomial error distribution (McDonald & Rosina 2001, Del Bianco & Borgoni 2006). Death events were modelled according to mean wind speed, a dichotomous variable accounting for occurrence of rainfall events during each interval (rainfall, hereafter), temperature residuals, nestling hatching date and age, and mean number of nestlings at a nest during each interval. In addition, preliminary inspection of the data suggested that probability of death steeply increased for fourth-hatched nestlings (see Fig. 2a). Therefore we also included among the predictors the interaction between mean number of nestlings and hatching order. Nest and nestling identity were included as random factors to account for repeated observations of the same nestling and for non-independence of data from the same brood. Nestling sex was not included among predictors in this analysis because ten nestlings died at a very young age before the blood sample for molecular sexing could be taken and excluding individuals that died very young could have potentially biased the results of this analysis. The analysis was performed with the *glmer* procedure in the *lme4* (Bates *et al.* 2012) package in R 3.0.2 (R Core Team 2013).

### Growth curves

We discarded from the analysis all the individuals that prematurely died or disappeared from the nest because

their growth patterns may not reflect those of nestlings that successfully fledged. We also discarded from this analysis 16 nestlings from 12 nests that we were unable to molecularly sex.

To model nestling growth we used curves of the double-Richards family, which are described by the general equation:

$$y = \frac{A}{[1 + m e^{-k(t-i)}]^{\frac{1}{m}}} + \frac{A'}{[1 + m' e^{-k'(t-i')}]^{\frac{1}{m'}}}, \quad (1)$$

where  $y$  is the estimated mass at age  $t$ ,  $A$  and  $A'$  are the asymptotes of both increasing and decreasing curves;  $k$  and  $k'$  are the rates at which the slope of both curves changes with age;  $i$  and  $i'$  are the inflection points, corresponding to the age at which the nestling shows its fastest growth (or weight recession);  $m$  and  $m'$  are the shape parameters of the generalized logistic curves.

The widespread application of these curves in the ornithological literature has been hampered by computational difficulties in fitting non-linear regression models. Recently, a new package called *FlexParamCurve* (Oswald *et al.* 2012) has been released for the software R (R Core Team 2013). This package allows fitting 32 possible growth curves of the double-Richards family (all possible reductions in the second curve, fixing  $A'$ ,  $k'$ ,  $i'$  or  $m'$  both when  $m$  is fixed or estimated). This package also provides automatized routines for assessing which curve, among the 32



alternative parameterizations of the double-Richard curve, best fits the data at hand (Oswald *et al.* 2012).

We used the *pn.modselect.step* routine to identify the parameterization of the double-Richards curve that best fitted our data (see Oswald *et al.* 2012 for details).  
 260 This routine selected a curve where parameters  $A$ ,  $k$ ,  $i$ , of Equation 1 varied among individual nestlings, while the other five were fixed to their mean value among all nestlings (curve # 32 of the *FlexParamCurve* package).  
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We used a Non-Linear Mixed Model (NLMM), whereby nestling body mass at each visit was modelled as a double-Richard curve of nestling age, for investigating whether variation in the three parameters of the curve that differed among nestlings was affected by sex, hatching date, hatching order of each nestling ('nestling features' hereafter) and mean brood size. In these analyses, and differently from the other models, mean brood size was calculated as the mean number of nestlings present at *all* the visits at the nest, because only covariates that did not vary within nestling could be entered in this model. Nestling and nest were entered as random grouping factors. NLMMs allow large flexibility in the model parameterization because it is possible to model any parameter of the growth curve as a function of different predictors. This flexibility extends also to the random part of the model, because it is possible to enter different random structures for each parameter of the growth curve.  
 270  
 275 However, NLMMs are challenging statistical tools. To reduce the complexity of these models we ran preliminary analyses to assess which (combination of) predictor(s) seemed to affect each of the three parameters of the growth curve that differed among nestlings.  
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To assess the structure of both the fixed and the random part of the NLMM we first interpolated double-Richards curves (curve #32; Oswald *et al.* 2012) to weight data of each nestling separately and noted the value of the estimated parameters. We then included each parameter as dependent variable in separate Linear Mixed Models (LMMs), where brood size, sex, hatching date and hatching order were entered as predictors, while nest was entered as a random effect. Significant predictors were noted, and these pieces of information were used to build the fixed part of the final NLMM. We also re-ran the same models by removing the random nest effect, and compared their fit with that of LMMs by means of the Akaike's Information Criterion. If the LMM had a lower AIC than the corresponding linear model (LM),  
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then nest was entered as a random factor for that parameter in the final NLMM.

Finally, repeated measures of the same nestling often show temporal autocorrelation, and variance in nestling weight also usually increases with nestling age. In the final NLMM we therefore assumed a residual autocorrelation with lag up to ten days, and a variation of the variance with age according to an exponential function, as suggested in Oswald *et al.* (2012).

LMMs and LMs were fitted by the *lme* procedure and *gls* procedure in the *nlme* package (Pinheiro *et al.* 2013). NLMM was fitted by the *nlme* procedure in the *lme4* package. All the analyses were run in R 2.15.0.

### **Influence of weather conditions on nestling growth during the Linear Growth Phase**

To objectively identify the age range of the Linear Growth Phase, which is unknown for the Common Swift, we sought to identify the age range whereby a linear function best approximated the double-Richards curve identified in previous steps. To this end, we first identified, from the growth curve obtained in the previous analysis, the age when Common Swift nestlings grow at maximum rate (maximum of the first derivative of the double-Richards curve estimated as above with parameters set to the mean values of nestling features). We then fitted a linear function to the nestling weights estimated by the growth curve (one data point per day) for all the possible age intervals including the age when maximum growth rate was attained. The Linear Growth Phase was then estimated as the longest interval in which the linear function approximated the double-Richards curve with  $R^2 \geq 0.999$ . This procedure indicated that the Linear Growth Phase of Common Swift nestlings spanned from age 5 to 14 days.

We then selected only weights recorded during the Linear Growth Phase of each nestling and calculated nestling daily growth rates as the differences in body mass divided by the number of days between consecutive visits. Daily growth rates of each nestling were then modelled in a LMM assuming a Gaussian error distribution, including as predictors the linear and the squared term of residuals of temperature on date, occurrence of rainfall (dichotomous variable) and mean wind speed in the interval, together with sex, age and hatching order and mean number of nestlings present at the nest during the interval. The squared value of temperature residuals was entered because preliminary analyses suggested possible non-linear effects of

temperature, but not of wind speed, on nestling growth rate (details not shown). Temperature residuals were negatively correlated with rainfall ( $r = -0.46$ ) and with wind speed ( $r = -0.64$ ), while rainfall and wind speed were positively correlated ( $r = 0.49$ ). Nest and nestling identity were included as random grouping factors to account for repeated observations of the same nestling and for non-independence of data from the same brood. The analysis was performed with the *lmer* procedure in the *lme4* package in R.2.15.0, with degrees of freedom set conservatively equal to the number of nests included in the analysis.

## RESULTS

### Mortality

During the 2012 breeding season, 26 nestlings from 18 nests were either found dead (16 nestlings) or disappeared prematurely from the nest (10 nestlings), while 112 nestlings from 47 nests successfully fledged. The probability that a nestling died between two consecutive visits at a nest varied according to hatching order, mean number of nestlings present at the nest during the period between the visits and the interaction between these variables (Table 1). In particular, first-hatched nestlings had lower probability of dying than late-hatched ones (Fig. 2a). The probability of dying decreased with an increasing number of siblings (Fig. 2b). However, closer inspection of the coefficients indicated that fourth-hatched nestling had always the largest probability of dying. Furthermore, we re-ran the same analysis excluding the five nests with four nestlings. The

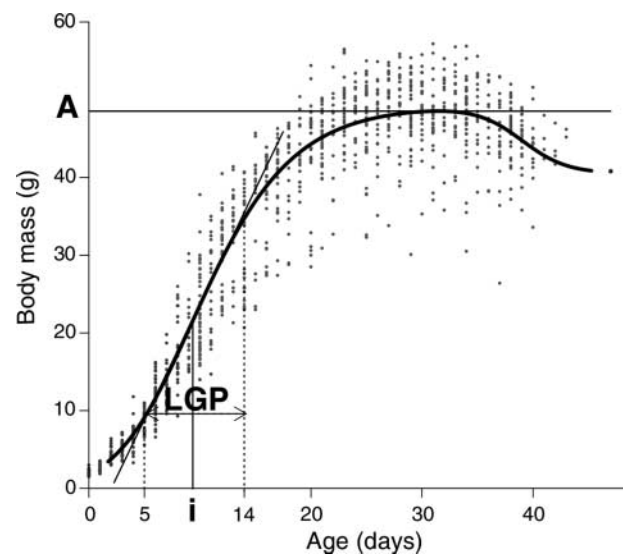
**Table 1.** GLMM of the effects of meteorological variables and nestling features on nestling mortality. Only estimates for fixed effects are shown. Nest and nestling identity were included as random factors in the model. Sample size is  $n = 1547$  observations from 138 nestlings and 65 nests. Mortality occurred in 26 nestlings (18.8% of the nestlings).

Effect	Coef.	se	z	P
Intercept	-7.558	0.804	-9.4	<0.001
Wind speed	-0.185	0.433	-0.4	0.67
Rainfall	-0.333	0.614	-0.5	0.59
Temperature residuals	0.196	0.179	1.1	0.28
Hatching date	0.042	0.047	0.9	0.38
Mean nestling age	-0.029	0.029	1.0	0.31
Hatching order	2.058	0.569	3.6	<0.001
Mean nestling number	-2.553	0.709	-3.6	<0.001
Hatching order $\times$ mean nestling age	1.825	0.439	4.2	<0.001

coefficients of this model showed that the interaction between hatching order and mean number of nestlings was no longer significant, while their main effects were confirmed (details not shown), thus indicating that in the model that included all of the data the significance of the interaction represented the steep increase in mortality of fourth-hatched nestlings. Collinearity among meteorological variables did not severely affect model coefficients, because models where each weather variable was included singly gave qualitatively similar results (details not shown).

### Growth patterns

Ninety-one nestlings (46 males and 45 females) from 44 nests fledged at an age  $>35$  days and could be molecularly sexed. Mean brood size was  $2.38 \pm 0.08$  se and mean hatching date was  $145.3 \pm 0.79$  se (24 May). Growth curves interpolated separately from data from each nestling indicated that maximum weight (parameter A of the Double-Richards curve – see Fig. 3 and Equation 1) was  $50.30 \pm 0.37$  se g on average, the rate at which the slope of the increasing part of the curve changed with age (parameter k) was  $0.21 \pm 0.01$  se  $\text{g day}^{-2}$  and mean inflection point of the curve (parameter i) occurred when nestlings were on average  $9.54 \pm 0.15$  se day old (Fig. 3).



**Figure 3.** Body mass of nestlings that fledged successfully (light grey points) in relation to age. A double-Richards growth curve #32 (Oswald *et al.* 2012) was drawn using the coefficients of the NLMM shown in Table 2 and the mean brood size and hatching date of the population. Parameters A, and i of the double-Richards curve are shown, as well as the Linear Growth Phase.

**Table 2.** Final NLMM for the growth curves. The statistically significant effects are shown for each of the three parameters of the double-Richards curve. A: maximum weight;  $k$  = rate at which the slope of the increasing part of the curve changes with age;  $i$  = mean inflection point (see also Fig. 3 for a graphical description of the parameters). Nest identity was included as a random factor for parameters A and  $i$  while nestling identity was included as a random factor for parameters A,  $k$  and  $i$  (see Methods for details). Sample size is 1031 observations for 91 nestlings belonging to 44 nests.

Effect	Coef.	se	df	$t$	$P$
A	49.243	0.435	966	113.1	<0.001
A × hatching date	-0.192	0.055	966	-3.5	<0.001
A × brood size	-2.198	0.818	966	-2.7	0.01
$k$	0.207	0.004	966	48.76	<0.001
$k$ × hatching date	0.003	0.001	966	5.2	<0.001
$i$	9.256	0.124	966	74.4	<0.001
$i$ × hatching date	-0.120	0.017	966	-7.2	<0.001

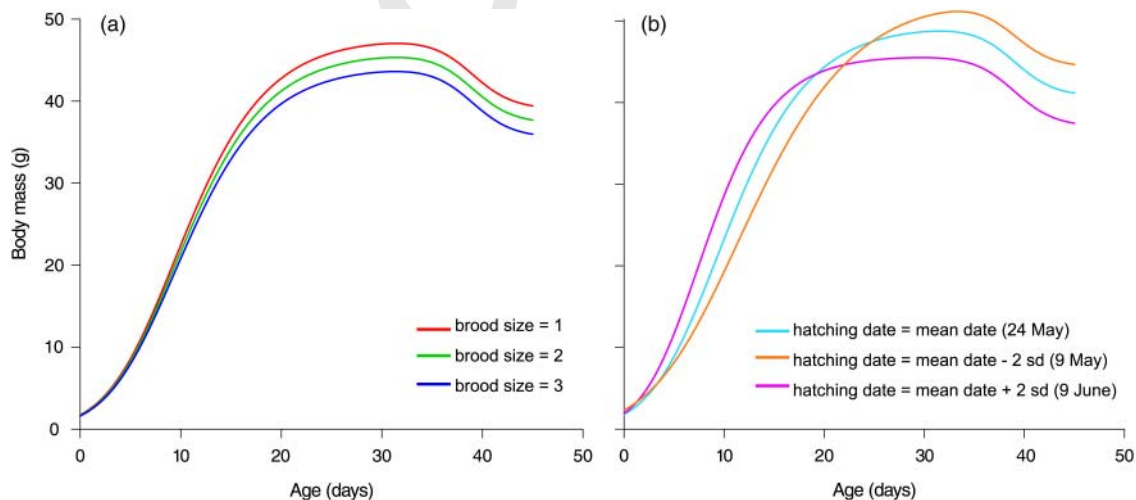
The coefficients of the final model (Table 2) indicated that nestlings in late broods, on average, grew faster (negative effect of hatching date on parameter  $k$ ) and experienced the fastest growth rate at a younger age (negative effect of hatching date on parameter  $i$ ) than those of early broods (Table 2, Fig. 4). These nestlings, however, reached a significantly lower maximum weight than nestlings born early in the season (negative effect of hatching date on parameter A, Table 2, Fig. 4). In addition, the maximum weight reached by nestlings of large broods was significantly lower than that reached by nestlings of small broods (negative effect of brood size on parameter A, Table 2, Fig. 4). Significant differences among nestlings in growth patterns, therefore, are produced by features

that are shared or very similar between all siblings in a nest, namely brood size and hatching order. Indeed individual features, namely sex and hatching order, did not affect growth curve parameters.

### Linear Growth Phase, weather conditions and growth rates

The Linear Growth Phase occurred between 5 and 14 days of age for nestlings. Daily growth rates were calculated for 191 intervals from consecutive body mass measures of the 91 nestlings considered in previous analyses. Mean daily growth rate during the Linear Growth Phase was  $2.97 \pm 0.11$  se  $\text{g day}^{-1}$  (min =  $0.6 \text{ g day}^{-1}$ , max =  $7 \text{ g day}^{-1}$ ). Overall, Linear Growth Phases occurred between 18 May (day 139) and 4 July (day 186). On these days mean daily temperature was  $23.6 \pm 0.6$  se  $^{\circ}\text{C}$ , with a minimum value of  $9.5 \text{ }^{\circ}\text{C}$  registered on 19 May and a maximum value of  $35.0 \text{ }^{\circ}\text{C}$  registered on 1 July. Rainfall occurred in 9 out of 48 days. Mean daily wind speed was  $1.45 \pm 0.07$  se  $\text{m s}^{-1}$ , with a maximum hourly value of  $6.8 \text{ m s}^{-1}$  recorded on 21 May.

Nestling growth rate varied non-linearly with the residuals of mean temperature on date, with nestlings growing significantly faster when residuals of temperature had intermediate values (Table 3, Fig. 5a). In particular, coefficients of the model indicated that nestlings grew faster when temperature was  $0.52 \text{ }^{\circ}\text{C}$  higher than that expected from seasonal trend. Furthermore, significant and positive effects of rainfall and of mean wind speed indicated that nestlings grew significantly faster during



**Figure 4.** Double-Richards growth curves drawn using the coefficients of the NLMM (Table 2) at (a) mean hatching date of all broods considered but different values of brood size and (b) mean size of all broods, but different values of hatching date.

410 **Table 3.** LMM of the effects of meteorological variables and nestling  
 415 features on growth rates during the Linear Growth Phase. Only  
 estimates for fixed effects are shown. Nest and nestling identity were  
 included as random factors in the model. Sample size is 191  
 observations for 91 nestlings belonging to 44 nests.

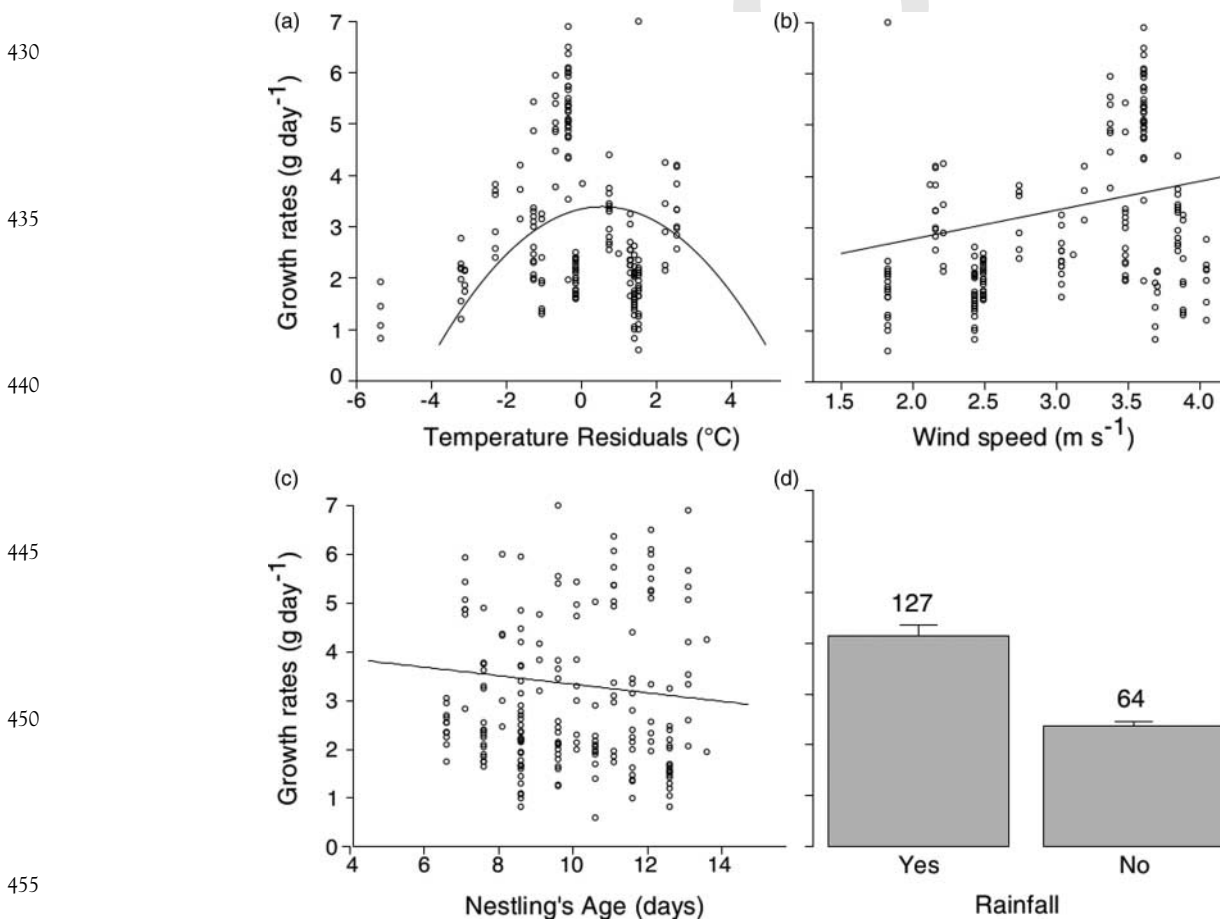
Effect	Coef.	se	df	t	P
415 Intercept	-1.385	2.157	42	-0.6	0.15
Date	0.024	0.013	42	1.8	0.08
Wind speed	0.579	0.152	42	3.8	<0.001
Rainfall	1.899	0.186	42	10.2	<0.001
Temperature residuals	0.138	0.072	42	1.9	0.07
(Temperature residuals) <sup>2</sup>	-0.133	0.020	42	-6.5	<0.001
420 Mean nestling age	-0.092	0.039	42	-2.4	0.03
Mean number of nestlings	-0.043	0.179	42	-0.2	0.39
Hatching order	-0.048	0.106	42	-0.5	0.36
Sex	-0.180	0.156	42	-1.2	0.20

425 intervals when wind was moderate (Table 3, Fig. 5b) and  
 when rain events occurred (Fig. 5d). Collinearity among  
 meteorological variables did not severely affect model

coefficients, because models where each weather variable  
 was included singly gave qualitatively similar results  
 (details not shown). Finally, a negative effect of mean  
 age suggested that, after controlling for the other effects,  
 growth rate of *individual* nestlings significantly decreased  
 with age (Table 3, Fig. 5c).

## DISCUSSION

Here we investigated the influence of the rearing  
 environment on the first stages of life of Common  
 Swift nestlings breeding in artificial nest boxes in  
 Northern Italy. We analysed the possible effects of  
 meteorological conditions, nestling features (sex and  
 hatching date and order) and number of nestlings at a  
 nest, which was used as a proxy for the strength of  
 competition for resources between siblings, on  
 nestlings' survival until fledging and growth patterns.  
 We analysed the effect of these factors both along the



**Figure 5.** Growth rates in relation to (a) the residuals of temperature on date; (b) wind speed; (c) mean nestling's age. Curves were fitted according to coefficients reported in Table 3. (d) Mean growth rates measured during intervals with and without rainfall events. Bars represent standard errors and numbers represent sample sizes.

460 entire pre-fledging period, including the physiological  
body mass recession that takes place before fledging,  
and in detail during the Linear Growth Phase, when  
growth rate is maximal.

465 Previous studies on Common Swifts have suggested  
that temperature, rainfall and wind speed negatively  
influenced the survival of Common Swift nestlings  
during the rearing period. Lack & Lack (1951) showed  
that nestling mortality in a breeding colony in Oxford  
(UK) was higher in poor weather conditions and in  
470 the same breeding colony Martins & Wright (1993)  
observed a significant brood reduction event in a  
single year of harsh weather. In Scotland, Thomson  
*et al.* (1996) found that breeding success was  
negatively correlated with mean temperature in June.  
475 Conversely, we found no effect of rainfall, temperature  
and wind on nestlings' mortality. This difference in  
the effect of meteorological conditions on nestling  
mortality should however be interpreted in the light of  
the general climatic conditions of the Po River Plain,  
480 where our breeding colony is located. Indeed, spring is  
typically warm in this area (mean May temperature in  
the study area was 18.9 °C in 2012), the summer is  
hot (mean July temperature was 25.9 °C in 2012, see  
also Fig. 1) and it is one of the less windy regions  
485 in Italy (according to the Italian Interactive Wind  
Atlas, [www.atlanteoelico.rse-web.it](http://www.atlanteoelico.rse-web.it) accessed on 10  
May 2013; the range of daily average wind speeds we  
observed was between 1.04 m s<sup>-1</sup> and 9.0 m s<sup>-1</sup>,  
corresponding to grade 1 ('light air') to grade 5 ('fresh  
490 breeze') in the Beaufort scale, see also Fig. 1). These  
climatic conditions differ from those of the UK, where  
most of the other studies on the Common Swift were  
conducted, where the summer is fresh and wet (in  
June 2012 in Oxford mean air temperature was 17.1°C  
495 and total rainfall was 151.7 mm, according to data  
collected at the Radcliff Meteorological Station and  
available at [www.geog.ox.ac.uk](http://www.geog.ox.ac.uk)). Therefore, it is likely  
that the meteorological conditions considered in this  
study showed only modest variation during the period  
500 when our study was carried out, that did not affect  
nestlings' survival. Alternatively, the effects of  
weather conditions on nestling survival may vary  
markedly among populations breeding in different  
geographical areas of Europe (Rajchard *et al.* 2006), or  
505 may depend on the general climatic condition of  
the region where the colony is located (Salewski *et al.*  
2013).

In our analysis of nestling survival we also accounted  
for competition for resources among siblings, the  
510 intensity of which was summarized by the number of

nestlings present at a nest during the interval between  
two consecutive visits, for hatching order, nestling age  
and hatching date which may reflect seasonal variation  
in parents' quality (see Hasselquist & Kempenaers  
2002 for a review). We found that nestling mortality  
increased with hatching order, probably as a result of  
intra-clutch hierarchies and domination of older  
siblings over younger ones. O'Connor (1979) showed  
that in the Common Swift, nestlings hatched from last  
eggs had reduced survival prospects, due to failure in  
competition for food with older, larger siblings. This  
has been confirmed by behavioural observations of  
food distribution in the closely related Pallid Swift, AQ7  
which showed that last hatched nestlings obtained less  
food than their older siblings, and, consequently, were  
the more likely to die (Malacarne & Cucco 1991,  
Malacarne *et al.* 1994). In our study the number of  
siblings at a nest, however, seemed to enhance, rather  
than reduce, nestlings' survival prospects. This may be  
due to variation in parental quality, with larger broods  
being reared only by experienced or high quality  
parents (Clutton-Brock 1988, Newton 1989).  
However, fourth-hatched nestlings always had the  
lowest survival rate. This is consistent with previous  
observations of Common Swifts where four nestlings  
fledge successfully only very rarely (Perrins 1964,  
Martins & Wright 1993). Finally, after accounting for  
the effects of the other variables, we observed that  
nestling age did not affect survival. This result was  
unexpected because in birds survival usually increases  
with nestling age (at least up to fledging, Peak *et al.*  
2004, Grant *et al.* 2005), and we have no clear  
explanation for it.

In the second part of our work we detected a  
significant inter-individual variability in growth  
patterns in the phase of weight increase, but not in  
that of the pre-fledging mass loss, as indicated by the  
fact that the parameters of the decreasing part of the  
growth curve did not vary significantly among  
nestlings. Moreover, nestlings from late broods, on  
average, grew faster and experienced the fastest growth  
at a younger age than those of early broods. This  
finding corroborates the idea that nestling growth is a  
flexible trait that can be adaptively modified to match  
environmental conditions (Mainwaring *et al.* 2010).  
Common Swifts have a tightly scheduled reproductive  
season (Cramp 1998): adults arrive at breeding sites in  
Northern Italy in mid-April and depart for Africa at  
the end of July together with newly fledged nestlings,  
which leave for their winter quarters almost  
immediately after fledging (Cramp 1998). Such tightly

scheduled reproductive activity may have favoured the evolution of rapid early growth in nestlings from late clutches, which may allow them to be ready to migrate in a shorter time. Indeed model coefficients indicated that a hypothetical nestling hatched on May 9 (the mean hatching date of the colony minus 2 sds) reached its maximum weight at 34 days of age, while a nestling born on June 9 (the mean hatching date of the colony plus 2 sds) reached its maximum weight at 30 days of age. However, rapid early growth may be at a cost of pre-fledging body mass. Indeed, nestlings born late in the season reached a lower maximum weight than those hatched earlier (the predicted difference in maximum weight between a nestling hatched on May 9 and one hatched on 9 June is 5.64 g corresponding to 11.2% of the mean maximum weight of nestlings estimated by the double-Richards curve). This difference also implies that late-hatched nestlings reached a lower body mass at fledging, because body mass recession (parameter A') did not vary among nestlings in our study population. This could severely affect the fitness of late-hatched nestlings because many studies have indicated that body mass at fledging is a good proxy of future survival in birds (Perrins 1965, Gustafsson & Sutherland 1988, Tinbergen & Boerlijst 1990, Wright *et al.* 2006).

Maximum weight was also significantly lower in fledglings from larger broods which was expected because of a higher competition for food among nest mates in larger broods. Indeed, Martins & Wright (1993), with an experimental manipulation of brood size, showed that the amount of food delivered by parents to each nestling decreased with brood size in Common Swifts. However, the difference in maximum weight among nestlings grown in broods of two or three nestlings is equal to only 1.6 g (i.e. 3.2% of maximum weight) on average according to model-predicted values.

Finally, sex and hatching order did not affect variation of growth patterns between individuals. The fact that male and female nestlings did not show any significant difference in their growth patterns is not surprising for a sexually monomorphic species like the Common Swift, although other studies on size-monomorphic species have found some differences in growth between sexes (see, for example, Rosivall *et al.* 2010 on the collared flycatcher *Ficedula albicollis*).

Conversely, the finding that hatching order had no significant effect on growth trajectories was surprising, and may be due to the fact that for the analyses of growth patterns we considered only nestlings that successfully fledged and therefore excluded from the

analyses all fourth-born nestlings, because none of them successfully fledged in the reproductive season of 2012. This selection could have potentially prevented our ability to reveal any effect of hatching order on growth patterns. We stress, however, that on the one hand, information on all nestlings that were found dead or that prematurely disappeared from the nest was considered in the previous analysis of mortality. On the other hand, growth trajectories of nestlings that were in very poor condition and that died prematurely were graphically inspected and appeared markedly aberrant compared to those of successfully fledged nestlings (details not shown). Their inclusion in an analysis of 'normal' growth rates was therefore untenable.

We note that all the features that appear to produce significant differences in growth patterns among nestlings, namely hatching date and brood size, were shared between all siblings in a nest. Hence, our results suggest that differences in the rearing environment among broods or in parental quality are more relevant in influencing nestlings' growth than nestlings' individual quality or ability to compete for food with nest mates. Parents-offspring interactions may therefore be more important than sib-sib interactions in shaping Common Swift nestling growth trajectories.

In the last part of our study we investigated in detail the effects of weather conditions on nestling growth, focusing on the Linear Growth Phase of nestlings that successfully fledged. Growth rate is an excellent indicator of the effects of environmental condition on nestling fitness, because it varies on a temporal scale similar to that of variability in weather patterns (Richner 1989, McCarty & Winkler 1999). We found that Common Swift nestlings grew at faster rates on days when the temperature was close to that expected from the seasonal trend, whereas their growth was slower at temperatures above and below the seasonal trend. Moreover, growth was faster during rainy and windy days. Several studies have indicated that in the Common Swift the most important and critical factor affecting nestlings' growth is food supply (Lack 1947, Newton 1980, Martin 1987, 1995). In a strictly aerial insectivore like the Common Swift, flying prey availability and adults foraging effectiveness are the major determinants of the amount of food received by nestlings, and both can be strongly affected by weather conditions. Indeed, aerial insect abundance is influenced by flight activity in response to weather (Taylor 1963, Lewis 1967, Johnson 1969, Pedgley 1990, Peng & Sutton 1992, Poulsen 1996) and also the flight performance and general physical condition of adults can

be affected by heavy rainfall (Ortega-Jimenez & Dudley 2012) or intense wind (Richardson 1978, Schmaljohann & Naef-Daenzer 2011). Thus, our findings may seem contradictory compared to the existing evidence. However, local climate conditions seem to affect the relationship between meteorological conditions and food provisioning to nestlings. For instance, in hot and sunny climates, with little or no rainfall and usually light winds, conditions which normally occur in the Po River Plain during May–July, the few moderately rainy days may trigger insect swarms because the insects may require some moisture in the air to survive (Gatehouse 1997). In addition, foraging Common Swifts may also benefit from moderate winds, because turbulent conditions may carry insects to high altitudes, where this species usually performs its foraging activity (Cramp 1998). The non-linear variation of growth rates of nestlings with temperature may reflect the natural variation of airborne insect abundance with temperature, which, for many taxa, increases with temperature up to an optimum and then shows a rapid decline (Williams 1940).

Overall, our results suggest that, in a geographical region where climate during the breeding season of Common Swifts is typically hot and characterized by high humidity and very little wind, meteorological conditions such as moderate rainfall or winds, do not influence survival of Common Swift nestlings, and may positively affect their growth. Furthermore, brood size and timing of breeding, which are under parental control, played a major role in influencing offspring survival and development. In contrast, brood size and timing of breeding were only marginally affected by features of individual nestlings, like their sex and order in the hatching hierarchy. Finally, our study highlighted that growth patterns of nestling Common Swifts show considerable seasonal plasticity, suggesting that they may be adaptively tuned to match the tight reproductive time schedule of this highly aerial species, which leaves for its African wintering range by late July–early August (Akesson *et al.* 2012). However, faster growth of late-hatched nestlings may not be cost-free, because it results in lower body mass at fledging, with potentially negative consequences on post-fledging survival. Indeed, during the early post-fledging phase, Common Swift fledglings may rely entirely on the energy reserves accumulated when in the nest, because parents are not known to provide care to their offspring once they have left the nest (Cramp 1998). However, the relative fitness costs and benefits of phenotypic plasticity in growth patterns remain a matter of speculation.

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