Catch-up growth strategies differ between body structures: interactions between age and structure-specific growth in wild nestling Alpine Swifts

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Summary

1. Little is known on the occurrence and magnitude of faster than normal (catch-up) growth in response to periods of undernutrition in the wild, and the extent to which different body structures compensate and over what timescales is poorly understood.

2. We investigated catch-up growth in nestling Alpine Swifts, *Apus melba*, by comparing nestling growth trajectories in response to a naturally occurring 1-week period of inclement weather and undernutrition with growth of nestlings reared in a good year.

3. In response to undernutrition, nestlings exhibited a hierarchy of tissues preservation and compensation, with body mass being restored quickly after the end of the period of undernutrition, acceleration of skeletal growth occurring later in development, and compensation in wing length occurring mostly due to a prolongation of growth and delayed fledging.

4. The effect of undernutrition and subsequent catch-up growth was age-dependent, with older nestlings being more resilient to undernutrition, and in turn having less need to compensate later in the development.

5. This shows that young in a free-living bird population can compensate in body mass and body size for a naturally occurring period of undernutrition, and that the timing and extent of compensation varies with age and between body structures.

Key-words: Apodidae, compensatory growth, developmental plasticity, food shortage, sibling competition

Introduction

The pattern of growth that an individual shows is determined by its genetic make-up and by environmental circumstances encountered during ontogeny (Starck & Ricklefs 1998). Evidence is accumulating that the environment experienced in early life has a substantial influence on phenotypic quality at adulthood, and in turn on future reproduction and longevity (Lindström 1999; Bateson *et al.* 2004). Since food is the fuel for growth and development, the quantity and quality of the feeding regime in early life are viewed as major environmental factors shaping growth and lifetime reproductive fitness (Festa-Bianchet, Jorgenson & Reale 2000). For example, in the Carrion Crow, *Corvus corone*, food limitation during the nestling phase reduces growth and final size of the skeleton, which in turn can prevent the acquisition of a breeding territory and hence

strongly impair breeding success, small individuals being out-competed by larger opponents (Richner 1989, 1992). Consequently, because the production of a sub-optimal phenotype (in the light of its genetic potential) can have dramatic fitness consequences (Lindström 1999; Bateson *et al.* 2004), organisms are predicted to have evolved compensatory strategies to minimize the cost of temporary poor rearing conditions (Metcalfe & Monaghan 2001). To compensate for the negative impact of poor nutrition on growth, organisms have evolved the capacity to accelerate development once food is again freely available (hereafter referred to as 'catch-up growth') and/or to delay the maturation of specific tissues as long as food is short and in turn to extend the developmental window (Schew & Ricklefs 1998; Metcalfe & Monaghan 2001; Bize *et al.* 2003).

Although catch-up growth is a well-known phenomenon in domesticated animals (Schew & Ricklefs 1998) and in wild animals with indeterminate growth such as turtles and fishes (Bjorndal *et al.* 2004; Álvarez & Nicieza 2005; Johnsson & Bohlin 2006), there is limited

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evidence in nature that organisms with determinate growth such as birds and mammals can catch up in size following a period of undernutrition (Nilsson & Svensson 1996; Royle 2000; Bize *et al.* 2003). Four mutually non-exclusive reasons may account for difficulties in documenting catch-up growth in nature in animals with determinate growth. First, the effects of undernutrition and subsequent catch-up in size can vary with age and developmental stage, with early stages being usually more sensitive to periods of undernutrition (Desai & Hales 1997) and thus, probably, more likely to subsequently catch up in size. Since in the wild it is more difficult to monitor early than late developmental stages (especially in mammals), the lack of evidence for catch-up growth can be linked to methodological rather than biological constraints. Second, different tissues, organs and morphological traits can contribute differentially to fitness, and hence the hierarchy of protection and compensation of each structure should vary according to their contribution to fitness at a given stage (Metcalfe & Monaghan 2001). To survive prolonged periods of food shortage, organisms rely on lipids stored in fat tissues and on proteins catabolized from internal organs such as pectoral muscle, gut and liver. Because these body reserves shrink during periods of undernutrition (Nicieza & Metcalfe 1997) and reserves are key to ensure maintenance and survival, body reserves and especially proteins from vital organs should be preserved at the expense of growth in body size in periods of undernutrition, and they should also be more rapidly restored than any compensation in body size following a period of undernutrition (Álvarez & Nicieza 2005; Johnsson & Bohlin 2006). This implies that there can be structure-specific catch-up growth strategies within organisms (Fortman, Reichling & German 2005), and thus growth trajectories of more than one trait need to be compared. Third, catch-up growth does not always occur immediately following the end of the period of undernutrition (i.e. short-term catch-up growth) and can take place at some later time in development (i.e. long-term catch-up growth; Mangel & Munch 2005). Simulations of catch-up growth based on a life-history model pointed out that long-term catch-up growth is probably more likely than short-term catch-up growth (Mangel & Munch 2005), and therefore to detect catch-up in size it may be necessary to monitor growth trajectories over the entire developmental period. Finally, when only a fraction of individuals within a brood or cohort suffer from undernutrition, individuals with a poor growth may never get the chance to catch up in size if undernutrition impairs their competitive abilities and subsequent access to resources (Royle 2000). Therefore catch-up growth may take place only when all individuals of a brood or cohort are simultaneously affected by undernutrition due to a sudden and broad environmental shift in resource levels, so that compensating individuals are not at a relative competitive disadvantage.

In the present study, we report growth and development in body mass, sternum size and wing length in nestling Alpine Swifts, *Apus melba* (Apodiformes), before, during and after a 1-week episode of rain and cold temperature, and we examine the occurrence and nature of catch-up growth by comparing their growth trajectories with data collected in the same colony in a year of prime weather and rearing condition. The Alpine Swift is a suitable model organism to study undernutrition and catch-up growth strategies because parents feed their young exclusively on aerial insects, so that the whole brood may be forced to fast for several consecutive days during periods of inclement weather (Arn 1960; present study), and because parental care ceases at fledging, implying that body mass and body size at fledging should be particularly fine tuned (Martins 1997). Nestlings have completed their development when they take their first flight at an age of 51–76 days (Bize *et al.* 2003). We also investigated whether catch-up growth strategies varied with age. We predicted that younger nestlings should be more sensitive to food deprivation, and in turn more likely to exhibit catch-up growth once environmental conditions improve, compared with older ones. Second, because the survival of dependent young relies first of all on their body reserves and on the correct functioning of internal organs, we predicted that catch-up in body mass (which correlates with body reserves and provides a composite measure of lipid and protein reserves; Piersma & Jukema 2002) should be prioritized over compensation in body size (Álvarez & Nicieza 2005), and in turn that nestlings should be more prone to exhibit short-term catch-up in body mass and long-term catch-up in size. Finally, because in birds wing feathers are moulted at adulthood whereas bone sizes are inflexible, we predicted that there should be a stronger tendency for nestlings to catch up in skeletal size than in wing length.

Materials and methods

Fieldwork was carried out as part of a long-term study (since 1999) in an Alpine Swift colony of *c*. 50 breeding pairs located under the roof of a clock tower in Solothurn, Switzerland. Each year, nests were visited daily to determine clutch size and hatching date of the first egg (denoted day 0). We returned to nests at days 10, 20, 30, 40 and 50 after hatching (fledging takes place at 50–76 days of age; Bize *et al.* 2003) to measure body mass of each nestling to the nearest 0·1 g, sternum length to the nearest 0·1 mm and wing length to the nearest mm. Nestlings were individually recognized by marking them with a colour marker at hatching and by ringing them with a numbered ring at 10 days after hatching.

This paper compares the growth trajectories of nestlings in 2003 and 2005. In 2003 nestlings experienced the warmest summer in the last 20 years in Switzerland (Swiss meteorological station, media communication), and in turn the fastest development and highest peak body mass recorded between 1999 and 2005 (P. Bize, unpublished results). This year is thus taken to represent the growth of nestlings in ideal conditions. In contrast,

in 2005 nestlings experienced a 1-week period of rain and cold temperature between 4 and 10 July that caused unusually high mortality (23 out of 86 [26·7%] nestlings died during this interval of time) in comparison with the mortality rate observed in 2003 (5 out of 90 [5·6%] nestlings died throughout the entire nestling period; Fisher exact test, $P < 0.0001$). Nestling mortality in 2005 was due foremost to parents that abandoned their brood during the 1-week episode of inclement weather, and in turn to complete brood failure ($n = 6$ broods containing a total of 14 nestlings). The occurrence of cold temperatures and rain negatively affects the abundance of insects in the air, and nestlings in 2005 were not fed by parents for at least 2 consecutive days between 7 and 9 July (P. Bize, personal observation). Hence, comparison of nestling growth trajectories in 2003 and 2005 provides an ideal opportunity to investigate effects of a naturally occurring acute period of low food availability on the development and growth of wild organisms, and on the occurrence and magnitude of compensatory growth strategies following this period of undernutrition. In 2005 nestlings were aged 13–24 days on 4 July (i.e. first day of the episode of inclement weather). Thus, to investigate if effects of undernutrition on nestling growth trajectory differ between young and old nestlings, we divided broods in 2005 into two rearing categories depending on whether nestlings were on average 15 (range 13–16) days of age on the first day of inclement weather (hereafter referred to as 'ED-nestlings' for 'early deficit nestlings'), or whether nestlings were on average 21 (range 19–24) days of age on the first day of inclement weather (hereafter 'LD-nestlings' for 'late deficit nestlings'). Nestlings from 2003 that experienced prime rearing conditions are referred to as 'ND-nestlings' for 'no-deficit nestlings'. Weather conditions experienced by ED- and LD-nestlings in 2005 and by ND-nestlings in 2003 are reported in Table 1. There was no difference between years in the mean body mass of parents during incubation and in the mean number and volume of eggs they produced (all *P*-values > 0·13). Hence, variation in nestling growth

trajectories between 2003 and 2005 was probably not confounded with differences between years in parental condition or reproductive investment.

Only nestlings that survived up to fledging were included in the statistical analyses. Specific observed growth rates (SGR_{obs}) of body mass, wing and sternum between age x and $x + t$ were calculated as $[\log_{10}(M_{x+t}) - \log_{10}(M_x)]/t$, where M_x and M_{x+t} are the initial and final measurements of body mass, wing or sternum at age x and $x + t$, respectively. We used $\log_{10}$ rather than ln transformation because it is easier to interpret values when plotted on a $\log_{10}$ scale than on a ln scale. Data were $\log_{10}$-transformed to homogenize variance when comparing traits that differ in size and to improve the fit of our statistical models. Because growth rate of a given trait between age x and $x + t$ is usually strongly related to its initial size M_x, we calculated specific expected growth rates (SGR_{exp}) between age x and $x + t$ for a given initial size M_x using slopes (β) and intercepts (α) of linear regressions of SGR_{obs} on M_x in ND-nestlings (Table 2; $SGR_{exp} = \alpha + \beta \times M_x$). Hence, SGR_{exp} of ED- and LD-nestlings is the growth rate they would have exhibited between age x and $x + t$ if they were size M_x at age x and did not experience a 1-week period of undernutrition (i.e. if they were reared in 2003). To allow comparison in growth rates between rearing categories and between body structures, we carried out statistical analyses on relative growth rates of ED-, LD- and ND-nestlings, calculated as $[(SGR_{obs} - SGR_{exp})/|SGR_{exp}|] \times 100$. Thus, mean relative growth rate of ND-nestlings is centred at 0%, and relative growth rate of ED- and LD-nestlings is the deviation in percentage from SGR_{obs} of ND-nestlings. There was no significant difference between rearing categories in the mean number of fledglings per brood (ND-broods: 2·45 ± 0·12 SE, ED-broods: 2·33 ± 0·19, LD-broods: 2·13 ± 0·13; Kruskal–Wallis test: $\chi^2 = 2.71$, df = 2, $P = 0.26$). In total, we compared growth trajectories of 76 ND-nestlings from 31 broods, 26 ED-nestlings from 12 broods, and 17 LD-nestlings from 8 broods; we controlled for the non-independence of nestlings from the same brood

Table 1. Mean (± SE) daily temperature and precipitation in relation to rearing categories and nestling developmental stages. Nestlings in 2005 encountered a 1-week period of inclement weather and undernutrition between 15 and 21 days of age (ED-nestlings) or between 21 and 27 days of age (LD-nestlings), whereas in 2003 they experienced prime rearing condition throughout development (ND-nestlings). ED-nestling developmental stages were divided into 1–14, 15–21 and 22–50 days of age (i.e. before, during and after the period of inclement weather, respectively). LD-nestlings were 1–20, 21–27 and 28–50 days of age before, during and after the period of inclement weather, respectively. To allow comparison between rearing categories, we calculated the equivalent weather conditions experienced by ND-nestling between 1 and 14, 15–27 and 28–50 days of age. Meteorological data were collected by a Swiss meteorological Station located in Wynau at 30 km from Solothurn

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Variable	Rearing category	Before period of inclement weather	During period of inclement weather	After period of inclement weather
Daily mean temperature (°C)	ED-broods	22·0 ± 0·0	14·8 ± 0·8	19·1 ± 0·0
	LD-broods	21·0 ± 0·2	14·8 ± 0·8	19·9 ± 0·1
	ND-broods	22·2 ± 0·0	21·4 ± 0·2	20·8 ± 0·1
Daily rain (min)	ED-broods	1·3 ± 0·0	5·4 ± 1·5	2·8 ± 0·0
	LD-broods	1·4 ± 0·1	5·4 ± 1·5	2·9 ± 0·2
	ND-broods	0·6 ± 0·1	2·3 ± 0·2	2·9 ± 0·1

Table 2. Linear regressions of specific observed growth rates of body mass, sternum or wing between age x and $x + t$ over body mass, sternum or wing at age x. The regressions are based on the growth of 76 nestlings that experienced prime rearing condition throughout development in 2003 (ND-nestlings). The use of quadratic terms did not improve the fit of our regressions, and therefore we restricted our analyses to linear regressions

Variable	Age interval	Slope	Intercept	r^2	F	P
Body mass	10–20 days	−0·042	0·095	0·39	48·24	< 0·0001
	20–30 days	−0·040	0·081	0·25	24·27	< 0·0001
	30–40 days	−0·068	0·139	0·41	51·86	< 0·0001
	40–50 days	−0·015	0·026	0·04	3·33	0·07
Sternum length	10–20 days	−0·043	0·074	0·46	61·26	< 0·0001
	20–30 days	−0·024	0·045	0·29	28·55	< 0·0001
	30–40 days	−0·048	0·078	0·63	126·17	< 0·0001
	40–50 days	−0·012	0·020	0·16	14·26	0·0003
Wing length	10–20 days	−0·043	0·109	0·69	164·72	< 0·0001
	20–30 days	−0·031	0·079	0·59	96·45	< 0·0001
	30–40 days	−0·037	0·093	0·65	136·58	< 0·0001
	40–50 days	−0·042	0·103	0·75	221·74	< 0·0001

Table 3. Mean (± SE) relative growth rate of body mass, sternum and wing length in relation to rearing categories and successive periods of growth. Nestlings were divided in three rearing categories depending on whether they experienced prime rearing conditions (ND-nestlings), undernutrition between 15 and 21 days of age (ED-nestlings) or undernutrition between 21 and 27 days of age (LD-nestlings). Relative growth rates are calculated as the deviation in percentage between observed growth rates (data from 2003 and 2005) and growth rates expected should nestlings have encountered prime rearing condition (data from 2003). Thus, relative growth rates of ND-nestlings are centred at 0. Differences between rearing categories in relative growth rates were tested with ANOVAs; columns with different letters indicate a significant difference in relative growth rate between rearing categories (post-hoc pairwise comparisons using the Tukey's HSD test). For example, between 10 and 20 days of age, ND- and LD-nestlings grew their body mass at a similar rate, whereas ED-nestlings were growing their body mass at a significantly slower rate than ND- and LD-nestlings. Significant P-values after Bonferroni adjustment for multiple testing are reported in bold

Variable	Age interval	Relative growth rate of			ANOVA		
		ED-nestlings	LD-nestlings	ND-nestlings	df	F	P
Body mass	10–20 days	−44·4 ± 4·4 a	−6·2 ± 6·0 b	0·2 ± 2·1 b	2,48	49·28	**< 0·0001**
	20–30 days	44·7 ± 8·8 a	−27·3 ± 18·7 b	3·6 ± 7·2 b	2,48	8·22	**0·0009**
	30–40 days	−5·6 ± 11·2 a	−21·4 ± 17·9 a	−3·0 ± 18·6 a	2,48	0·15	0·87
	40–50 days	57·9 ± 20·8 a	161·4 ± 41·6 b	1·3 ± 10·3 a	2,48	15·99	**< 0·0001**
Sternum length	10–20 days	−33·7 ± 2·9 a	−6·7 ± 1·6 b	−0·3 ± 1·4 b	2,48	78·05	**< 0·0001**
	20–30 days	8·9 ± 4·5 a	−22·2 ± 5·5 b	0·9 ± 1·3 a	2,48	19·84	**< 0·0001**
	30–40 days	14·7 ± 3·8 a	7·8 ± 6·3 a	−0·2 ± 2·6 a	2,48	4·64	0·014
	40–50 days	40·8 ± 10·9 a	40·9 ± 13·6 a	−0·3 ± 5·8 b	2,48	8·37	**0·0008**
Wing length	10–20 days	−25·1 ± 2·6 a	−1·5 ± 0·8 b	−0·2 ± 0·6 b	2,48	104·30	**< 0·0001**
	20–30 days	1·5 ± 2·3 a	−17·7 ± 3·2 b	−0·6 ± 0·9 a	2,48	26·03	**< 0·0001**
	30–40 days	−1·1 ± 0·9 a	−12·2 ± 1·5 a	0·2 ± 0·9 b	2,48	41·33	**< 0·0001**
	40–50 days	5·7 ± 3·6 a,b	13·4 ± 5·3 b	0·5 ± 1·3 a	2,48	5·62	**0·0064**

by using mean sibling values. Analyses were performed using JMP IN 4 (SAS Institute Inc., Cary, NC); tests are two tailed and P-values less than 0·05 considered significant. When multiple tests were performed, we adjusted significance levels for the number (k) of tests performed using the Bonferroni method (i.e. $P_{\text{adjusted}} = 0·05/k$). *A posteriori* comparisons in ANOVA models were made using the Tukey HSD test.

Results

At day 10 after hatching, which was before the period of inclement weather in 2005, there was no significant difference in body mass, sternum size and wing length

between nestlings of the three rearing categories (i.e. ND-, ED- and LD-broods; Fig. 1).

EFFECT OF UNDERNUTRITION ON ED-NESTLING GROWTH TRAJECTORIES

ED-nestlings had lower growth rates in body mass, sternum size and wing length between 10 and 20 days after hatching (i.e. during the period of poor weather) compared with the growth of ND-nestlings over the same age interval (Table 3; Fig. 2a). As a result, at 20 days of age ED-nestlings were lighter and smaller in size than ND-nestlings (Fig. 1). In agreement with the hypothesis that nestlings should rapidly restore their body reserves,
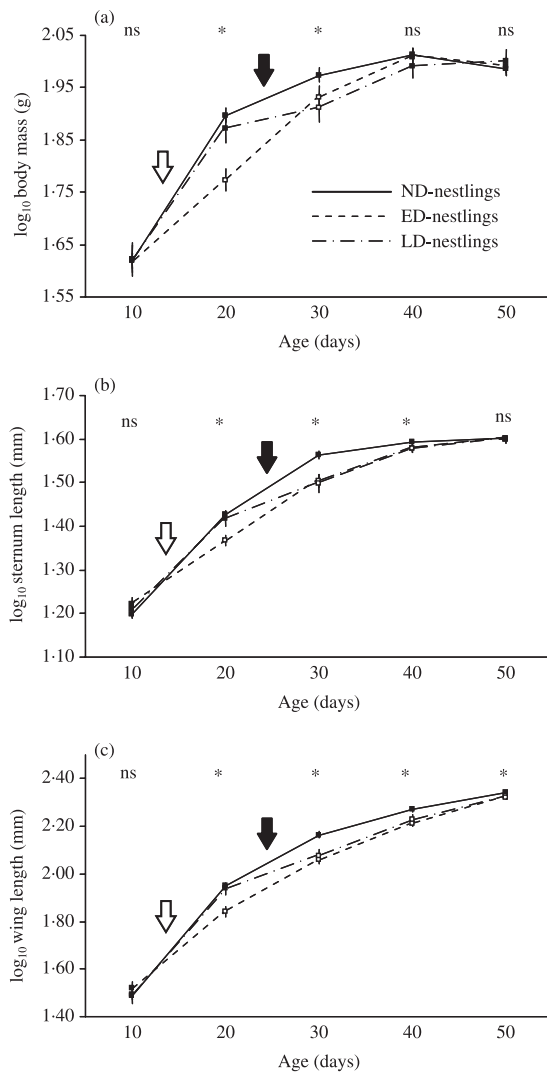
Fig. 1. Mean (±95% confidence interval) $\log_{10}$-transformed nestling (a) body mass, (b) sternum size and (c) wing length in relation to age and rearing categories. Nestlings in 2003 experienced prime rearing conditions (solid line; ND-nestlings) whereas in 2005 they encountered a 1-week period of inclement weather and undernutrition between 15 and 21 days of age (small-dash line; ED-nestlings) or between 21 and 27 days of age (large-dash line; LD-nestlings). The arrows indicate the age when ED-nestlings (white arrow) and LD-nestlings (black arrow) experienced the first day of inclement weather in 2005. Only nestlings that survived up to fledging were included in the statistical analyses. Repeated measures ANOVA on $\log_{10}$-transformed body mass at 10, 20, 30, 40 and 50 days of age shows that nestling body mass growth trajectories differ between rearing categories (age by rearing condition interaction: $F_{8,98} = 19 \cdot 66$, $P < 0 \cdot 0001$). Likewise sternum growth trajectories ($F_{8,98} = 17 \cdot 75$, $P < 0 \cdot 0001$) and wing growth trajectories ($F_{8,98} = 0 \cdot 26 \cdot 86$, $P < 0 \cdot 0001$) differed between rearing categories. Asterisks indicate significant differences between rearing conditions after Bonferroni adjustment for multiple testing (*$P_{adjusted} < 0 \cdot 001$; NS: $P_{adjusted} > 0 \cdot 01$), and squares with different colour (i.e. white *vs* black square) indicate significant difference in mass and size between rearing categories (post-hoc pairwise comparisons using the Tukey's HSD test). For example, at 20 days of age, ND- and LD-nestlings were similar in body mass, whereas ED-nestlings were significantly lighter than ND- and LD-nestlings.
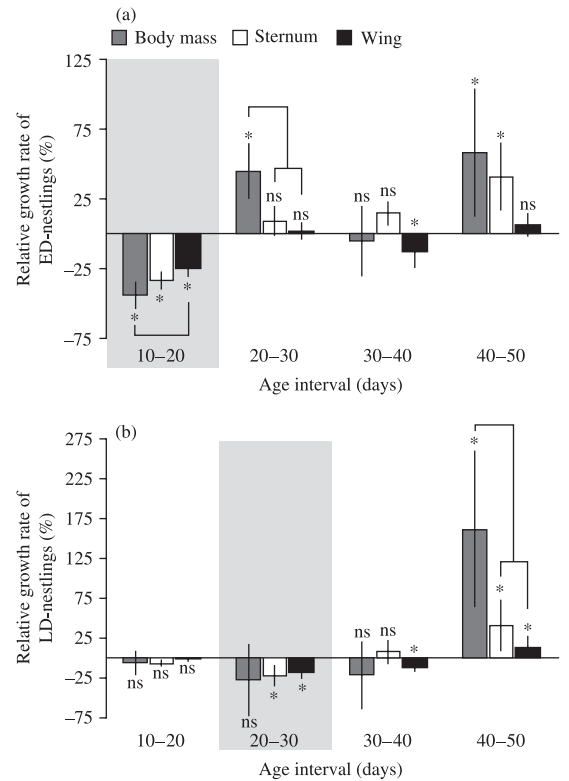
Fig. 2. Mean (±95% confidence interval) relative growth rate in body mass (grey bars), sternum size (open bars) and wing length (black bars) in nestlings that experienced in 2005 a 1-week period of inclement weather and undernutrition (a) between 15 and 21 days of age (ED-nestlings) or (b) between 21 and 27 days of age (LD-nestlings). The age interval when ED- and LD-nestlings experienced the naturally occurring period of undernutrition is indicated with pale grey shading. ED- and LD-nestling relative growth rate shows the percentage deviation from the growth of nestlings in 2003 that experienced prime conditions throughout development (ND-nestlings). For example, the +45% deviation in body mass growth rates between 20 and 30 days of age in ED-nestlings indicates that on average they were growing their body mass 1·45× faster than the average for ND-nestlings over the same age interval. Significant deviations in growth rates of ED- and LD-nestlings from growth rates of ND-nestlings are reported above the bars (*$P < 0 \cdot 05$; NS: $P > 0 \cdot 05$; statistical details are presented in Table 2). Line trees above the bars show significant differences in relative growth rates between body structures (mass *vs* sternum *vs* wing) after Bonferroni adjustment for multiple testing.

between 20 and 30 days of age (i.e. after the end of the period of poor weather) ED-nestlings quickly recovered in body mass by gaining mass at a significantly faster rate than ND-nestlings (Table 3; Fig. 2a). As a result of this short-term catch-up growth, by 40 days of age there was no significant difference in body mass between ED- and ND-nestlings (Fig. 1a). Before fledging, nestling swifts naturally lose an average of $7 \cdot 3 \pm 0 \cdot 3\%$ of their peak body mass ($n = 403$ fledglings measured in seasons 1999–2004; see also Arn 1960; Bize *et al.* 2003). Although both ED- and ND-nestlings lost body mass between 40 and 50 days of age (Fig. 1a), ED-nestlings lost less body mass than ND-nestlings ($3 \cdot 6 \pm 1 \cdot 2\%$ in

ED-nestlings *vs* 6·4 ± 0·6% in ND-nestlings; Table 3; Fig. 2a). This suggests that ND-nestlings at 50 days were more advanced in their tissue maturation and preparations for fledging than ED-nestlings, although the mean date of fledging of ED-nestlings is not known.

In agreement with the hypothesis that compensation in structural size has a lower priority than compensation in body mass (i.e. reserves), ED-nestlings exhibited long-term rather than short-term catch-up in sternum length: not until 40–50 days after hatching was their sternum growth accelerated in comparison with that of ND-nestlings (Table 3; Fig. 2a), but by 50 days of age there was no difference in sternum length between ED- and ND-nestlings (Fig. 1b). Note that ED-nestlings caught up in sternum size at an age when ND-nestling sternum growth was slowing to an asymptote (Fig. 1b).

In agreement with the hypothesis that there should be lower selection on nestlings to catch up in wing length compared with sternum length, at no time did the wings of ED-nestlings show accelerated growth above that expected for their length (Fig. 2a). Therefore the negative effect of inclement weather on nestling wing development remained perceptible throughout the study period and, at 50 days of age, nestlings still had shorter wings in ED- than ND-broods (Fig. 1c). However, the size deficit had decreased by this time, as a result of the wing growth of ND-nestlings slowing to an asymptote. Comparison of growth rates between body structures confirmed that mass and size of ED-nestlings responded differentially to the 1-week period of food shortage (Fig. 2a). There was a stronger reduction in the growth rate of body mass than of wings during the period of undernutrition, and body mass quickly accelerated in growth rate at the end of the period of undernutrition.

EFFECT OF UNDERNUTRITION ON LD-NESTLING GROWTH TRAJECTORIES

The 1-week period of inclement weather affected the growth of the sternum and wings of LD-nestlings in a similar manner to that of ED-nestlings. LD-nestlings had a reduced sternum and wing growth rate during the episode of inclement weather (i.e. between 20 and 30 days of age), and exhibited significant catch-up in both sternum and wing growth at the end of their development (i.e. between 40 and 50 days of age) (Table 3; Figs 1b,c and 2b). In agreement with the hypothesis that older nestlings may be less sensitive to (and better able to protect body reserves through) periods of inclement weather, the biggest difference between ED- and LD-nestlings was found in the growth and development of body mass, with LD-nestlings showing no significant slow-down in growth rate in body mass during the period of inclement weather, and in turn no short-term catch-up growth (Table 3; Figs 1a and 2b). The apparently higher rate of mass gain in LD-nestlings between 40 and 50 days shown in Fig. 2(b) was due to ND-nestlings losing mass over this time, rather than LD-nestlings showing any acceleration of mass gain. LD-nestlings were

the only group that did not lose mass between 40 and 50 days of age (Fig. 1a), suggesting that they were delaying the time of fledging compared with ED- and LD-nestlings. Accordingly, in 2005 we had measurements of age and wing length at fledging for the first 12 young that left the colony (12 out of 17 LD-fledglings, 71%), and comparison with the first 12 ND-young that left the colony in 2003 showed that LD-nestlings fledged at an older age (mean ± SE age at fledging in the first 12 nestlings that left the colony in ND- *vs* LD-broods = 51·5 ± 0·2 *vs* 57·1 ± 0·7 days; *t*-test: *t* = 7·36, *P* < 0·0001, df = 22) but with a similar wing length as ND-nestlings (mean ± SE wing length at fledging for the same ND- and LD-fledglings = 221·0 ± 1·3 *vs* 219·6 ± 1·7 mm; *t* = 0·63, *P* = 0·53, df = 22).

Discussion

The analysis and comparison of growth trajectories of Alpine Swift nestlings that experienced a 1-week period of inclement weather and undernutrition, either between 15 and 21 (ED-nestlings), or between 21 and 27 days of age (LD-nestlings), and nestlings that experienced prime weather and rearing conditions (ND-nestlings), show that species with determinate growth can naturally catch up in body mass and size in the wild (see also (Nilsson & Svensson 1996; Royle 2000; Bize *et al.* 2003). The finding that ED- and LD-nestlings exhibited short periods of accelerated size and mass growth compared with ND-nestlings suggests that nestling growth rate and development are optimized rather than maximized in nature and, as a consequence, that fast growth should be associated with long-term costs (Arendt 1997; Metcalfe & Monaghan 2001; Hales & Ozanne 2003; Mangel & Munch 2005). Finally, because effects of undernutrition on growth trajectories were age-dependent and structure-specific, our study highlights the importance of examining the effect of undernutrition on the development of multiple tissues/structure over several developmental stages.

STRUCTURE-SPECIFIC CATCH-UP GROWTH STRATEGIES

Because parents do not provide care after nestlings take their first flight and young have to spend the entire day on the wing after fledging (Bize *et al.* 2003), there should be strong selection on Alpine Swift nestlings to compensate in body mass and size before fledging. Furthermore, because body mass depletion in response to food shortage is associated with the use of lipid reserves from fat tissues and proteins from vital organs such as the gut or liver, nestlings should be more likely to exhibit rapid short-term catch-up growth in body mass than in sternum and wing length (Mangel & Munch 2005). Accordingly, depletion of body mass in ED-nestlings due to inclement weather and undernutrition between 15 and 21 days was followed by a short-term episode of catch-up growth in body mass between

20 and 30 days of age that allowed them to quickly restore their body mass and to reach a similar body mass as ND-nestlings by the age of 40 days. In contrast, sternum growth and wing growth were accelerated only at a later stage of development (40–50 days). This agrees with recent experimental findings in wild fish where food-restricted individuals restored their body mass relatively quickly (within 2 months of an improvement in food availability) (Álvarez & Nicieza 2005; Johnsson & Bohlin 2006), whereas catch-up in body length occurred later in development (5 months after the period of food restriction) (Johnsson & Bohlin 2006).

Since in birds the skeleton reaches its final size at the end of the developmental period whereas wing feathers are moulted at adulthood, we further predicted that there should be a stronger selection on nestlings to compensate through skeletal size than through wing length. Faster compensation in skeletal size than wing length is also predicted if a large skeletal size is important in sibling competition within the nest, so that a long sternum has a greater contribution to fitness at the nestling stage than well-developed wings (Royle 2000; Mangel & Munch 2005), and/or if fast growth of the sternum is less prone to errors and long-term damage than fast growth of feathers (Dawson *et al*. 2000; Mangel & Munch 2005). Accordingly, at 50 days of age we found that the sternum of ED- and LD-nestlings had fully caught up in size, whereas their wings were still smaller than those of ND-nestlings that had been well nourished throughout development. The partial catch-up in wing length by 50 days of age in ED- and LD-nestlings was explained by a weak acceleration of feather growth (13·4% *vs* 40·9% for the sternum) in LD-nestlings, but also by the fact that wing growth for ND-nestlings was slowing to an asymptote by this time. Thus, while ED- and LD-nestlings still had shorter wings at 50 days of age than ND-nestlings, it is still possible that wing length was fully compensated for at the time of fledging by extending the period of growth (for similar findings in the development of body size in fishes, see Royle, Lindström & Metcalfe 2005). Indeed, a previous manipulation of ectoparasite load in Alpine Swift nests showed that nestlings can compensate for parasite-induced reduction in wing growth rate not only by maintaining a higher than usual wing growth between 50 days of age and fledging, but also by growing their wings for a longer period of time and in turn by fledging at a latter age (Bize *et al*. 2003). The fact that ED- and LD-nestlings were losing body mass at a lower rate between 40 and 50 days of age compared with ND-nestlings suggests that ED- and LD-nestlings were delaying their fledging to allow full compensation in wing length. Accordingly, we found that the first LD-nestlings that left the colony did so at an older age than (but with a similar wing length to) the first ND-fledglings. Interestingly, LD-nestlings delayed their fledging by an average of 6 days compared with ND-nestlings, which coincides with the length of the inclement period.

AGE-DEPENDENT EFFECT OF UNDERNUTRITION AND SUBSEQUENT CATCH-UP GROWTH

During the 1-week episode of inclement weather and undernutrition, ED-nestlings gained significantly less mass than same-age ND-nestlings over the same time interval, whereas the mass gain in LD-nestlings was not significantly different from that of ND-nestlings. Since LD-nestlings sustained the growth of body mass during this period of undernutrition, while falling behind in sternum and wing growth, it suggests that body mass has a higher priority of tissue preservation compared with sternum and wing length (see also Bize *et al*. 2003), and that resilience to environmental stress increases with age. However, because tissues, organs and morphological traits can differ in their developmental windows and in turn in their sensitivity to environmental stressors, the hierarchy of tissue preservation and compensatory growth strategies might change during development. Hence, future work should be focused upon age-dependent variation in this hierarchy of tissue preservation and growth, and ultimately on age-dependent and structure-specific costs of compensatory growth. To this end, experiments are required where food availability is manipulated at different stages of development and the consequences monitored, in terms of both the growth trajectories of various tissues and body structures and the long-term outcomes.

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