

Developmental plasticity in a passerine bird: an experiment with collared flycatchers *Ficedula albicollis*

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Young birds often face poor food supply, which reduces their growth and development. However, if the shortage of resources is only temporary, there is a possibility to adjust the growth trajectory of morphological traits after the end of the short-term limitation period. The two main ways of compensatory growth are delayed development (parallel growth) and growth acceleration (catch-up growth). Parallel growth has been widely demonstrated in birds, but the presence of catch-up growth in altricial species has been questioned. However, most experiments have been conducted in laboratory conditions. We manipulated the food supply of nestling collared flycatchers *Ficedula albicollis* in the wild by removing the male parent for three days at 4–7 days of chick age. We performed early partial swapping to control for origin effects on growth, and total swapping after the period of food limitation to ensure similar late growth environment for deprived and control chicks. Both body mass and tarsus length of deprived chicks was negatively affected by the food scarcity. Body mass showed efficient catch-up growth, but this compensation was absent in skeletal size. Body mass is an important determinant of postfledging survival in this long-distance migrant. Further studies are needed in a variety of species to examine developmental plasticity in relation to age at food scarcity and the allocation hierarchy of various morphological traits.

The growth of body mass and body size in young birds is very rapid after hatching, which places considerable demands on the parents (Lindén and Møller 1989, Dijkstra et al. 1990, Török et al. 2004). A large part of the variation in breeding output among nests is caused by nestling mortality between hatching and fledging. Predictable environmental conditions and stable differences in individual quality can be taken into account when females decide how many eggs they lay in the current clutch (e.g. Petrie and Williams 1993, Pettifor et al. 2002). However, several factors may lead to poorer rearing conditions than predicted at egg-laying. Such factors include unpredictable food supply (Török et al. 2004), and reduced male care due to polygyny (Searcy and Yasukawa 1996), or extra-pair paternity (Dixon et al. 1994). Parents and chicks may also experience short-term limitations of food, for example due to adverse weather (Bryant 1975, Turner 1982).

If parents are unable or unwilling to compensate for the reduced food availability by increasing their feeding

rates, chicks will experience a general reduction of growth due to an insufficient supply of material and energy (phenotypic modulation; Smith-Gill 1983). The reduction of growth may have various adverse consequences, depending on the body parts involved. A permanently smaller body size due to early food limitation (Boag 1987) may impair later tolerance to nutritional stress (Merilä and Wiggins 1997), social rank in aggressive interactions (Dearborn and Wiley 1993), and mating success (Kempnaers et al. 1992). Reduced body condition before fledging, on the other hand, has been shown to affect the future prospects of nestlings in terms of survival (Tinbergen and Boerlijst 1990), reproductive performance (Haywood and Perrins 1992) and sexual ornamentation (Gustafsson et al. 1995). However, if the food shortage ends during the development of young, there is a possibility to compensate for the disadvantage in body condition or structural size. The intrinsic, adaptive potential of the chick to adjust the trajectories of growth

and trait maturation after the end of food restriction can be referred to as developmental plasticity (Schew and Ricklefs 1998). The study of developmental plasticity requires a detailed, preferably experimental, examination of the consecutive phases of development, which has rarely been undertaken (Emlen et al. 1991, Lepczyk and Karasov 2000, Bize et al. 2003).

The chick may compensate for the disadvantage in two non-exclusive ways. First, by slowing the maturation and prolonging the growth period of important organs, which also increases the time to independence (parallel growth; Bryant 1975, Emlen et al. 1991). Second, by increasing the speed of growth relative to age or developmental state, when resource supply returned to the normal level (compensatory or catch-up growth; Bohman 1955). Most investigations documenting flexibility in the speed of growth have been conducted in poultry (Schew and Ricklefs 1998). Studies of developmental plasticity in passerines sometimes found prolonged development, but accelerated growth was rarely detected (reviewed by Lepczyk and Karasov 2000). However, our understanding of the plastic growth responses of altricial birds is hampered by the fact that only a single study has been conducted in the natural breeding environment of the species (Bize et al. 2003). Field experiments more accurately mimic the situations faced by birds in real life than laboratory studies. For example, the composition of food given to laboratory birds almost certainly differs from that provided by the parents in the wild. The frequency and magnitude of food deprivation in a laboratory setting may also deviate from the natural pattern. Finally, the provisioning capacity of parents in the wild may limit the food intake of young even after the improvement of food conditions, so results from laboratory regimes with ad libitum or even surplus food may prove hard to extrapolate to natural situations. The problem can also be interpreted as a methodological trade-off between the experimental control of events and the generality of conclusions outside the experimental system.

Here an experimental field study is reported on developmental plasticity of nestlings in the altricial collared flycatcher *Ficedula albicollis*. First, partial cross-fostering was performed to control for genetic or early maternal effects on developmental plasticity, as well as for differences between breeding pairs in parental care levels or feeding ability. Second, temporary male removal was applied to induce food shortage. Third, the captive males were released and whole food-deprived broods were moved to nests where the parents had not been disturbed before. The last step was done to avoid any confounding effects of the temporarily elevated workload of widowed females or stress to removed males on their parental performance and thereby on offspring development. The control broods

were also moved to ensure a similar level of experimental manipulation to chicks in both treatments. Tarsus length and body mass were measured to see if developmental plasticity differed between the two traits. It was predicted that experimental broods would grow slower than controls during male removal. After male release and complete fostering, it was expected that the growth of previously deprived chicks would be faster than that of controls, if the respective body part was capable of catch-up growth. Otherwise, similar growth rates were expected in the two experimental groups. In both cases, the investigations targeted an age- and size-dependent developmental program, so growth increments at all age transitions were controlled for original size before the respective phase.

Methods

Study species and experimental protocol

The collared flycatcher is a small (ca 13 g), long-distance migrant, socially monogamous and hole-nesting passerine. Approximately ten percent of males are polygynous each year (Garamszegi et al. 2004). The experiment was conducted in Pilis Mountains, near Szentendre, Hungary, where a nestbox-breeding population of approx. 300 pairs has been studied since 1982. More details on the study area can be found elsewhere (Török and Tóth 1988). Collared flycatcher nestlings usually spend at least 14 days in the nest. Both parents take an equal part in the provisioning of nestlings. Male participation in chick feeding is important to reproductive success, as shown by the reduced performance of polygynous secondary broods (Garamszegi et al. 2004).

The study was done in the breeding season of 2005. The binary age of all males on the two experimental plots (yearling or older) was determined with binoculars by the colour of remiges and wing patch size (Svensson 1992, Török et al. 2003). Male age was important to this study because there are intrinsic differences in the growth of young from males of the two age classes (Hegyí et al. 2006a). Twelve trios of $n = 36$ synchronously hatched broods with males of similar age were selected where clutch size had been the same and all eggs had hatched. None of these nests was later identified as polygynous secondary. Two days after hatching, a partial cross-fostering was performed between two of the three nests in each trio (hereafter called nests A and B), with approximately half the nestlings exchanged. This step was done to investigate and control for origin-related similarities among nestlings, whether genetic or early maternal, and for the different parental quality of pairs. Chicks were individually marked by plucking tufts of down on the

head (Sheldon et al. 1998) and their body mass was measured.

At 4 d of age, nestling masses were taken in broods A and B, and the parents captured at one of the two nests (hereafter, A). Females were released after measurement, while males were kept individually in cloth-covered cages for the next three days. While in captivity, they were given mealworms *Tenebrio molitor* and drinking water ad libitum (Saetre et al. 1997, Slagsvold and Viljugrein 1999, Siitari et al. 2002). At 7d of nestling age, a complete swap was done using all three nests of the trio, to ensure that both experimental broods had the same rearing environment in the following. We thereby avoided differences in future growth between the treatment groups due to the disturbance to parents caused by the temporary widowing. At the time of transfer, nestlings were provided with numbered aluminium rings, and their body masses and tarsus lengths were measured. After this swap, the male of nest A was released from captivity.

At 10 d of nestling age, tarsus lengths and body masses were taken in the experimental broods (now in nests B and C). Parents at these nests were also caught and measured on this day. The mass and tarsus measurements of nestlings were repeated on day 12. Probably due to the rich supply of flying insects, the study year was characterized by rapid nestling development, and some of the experimental broods started to fledge as early as 13 d of age (our unpubl. data). Therefore, the 12 d measurements are considered here as prefledging data. Analyzing the smaller set of available data from 13 d of age yielded very similar results to those reported here. Body masses were taken with a Pesola spring balance, to the nearest 0.1 g. Tarsus lengths were measured to the nearest 0.1 mm with a caliper. Also measuring plumage traits such as wing length would have provided little additional information about compensatory growth, since they do not approach their asymptotic value by fledging (Rosivall et al. 2005). Fledging times were not recorded in this study. They are unlikely to have differed between the treatment groups (see Discussion).

Statistical procedures

The control treatment group analyzed included only chicks in nest C, but not those in nest A, because of the potential confound of stressed parents at the latter. Since the expectation was reduced growth in the food restriction period and gradually weakening compensation thereafter, the measured stages of growth were analyzed separately. Probability thresholds were Bonferroni adjusted to the number of tests applied. Generalized linear mixed models were used with normal error and identity link, as implemented in the GLIMMIX macro

of SAS 8.02. Nestlings that died during development were omitted from all analyses (5 young in 4 manipulated broods and 4 young in 3 control broods). Nestling measures and growth increments were used as dependent variables, treatment (restricted or control) as a fixed factor, and trio as well as nest of origin (nested within trio) as random factors. The factor trio allowed for the non-independence of broods within a foster unit due to temporal synchrony and spatial proximity. In case of growth increments, original mass/size was entered as a covariate. The binary age (yearling or adult) or the measured morphological and plumage traits of parents (see Török et al. 2003, Hegyi et al. 2006b) did not differ among treatment groups, except for female body mass, which was higher in the widowed nests than in the other groups, probably due to the earlier capture of these birds during the provisioning phase (data not shown). Entering female mass as a covariate did not affect the results of models presented below.

Rapid growth can be considered catch-up growth only if it is faster than expected from stage in the developmental program. If chick growth trajectories are regulated by current mass irrespective of age, correcting for age-specific original mass does not fully control for position on the growth curve. Therefore, a computer simulation was conducted to further explore whether any accelerated growth relative to controls observed in deprived chicks in the 7–10 d post-deprivation period is catch-up growth or only a consequence of different position of the two groups on the growth trajectory. In other words, there is no compensatory growth *sensu stricto* if deprived chicks grow faster than controls simply because they are still at a steep point on the growth curve. A logistic growth curve (Ricklefs 1967) was fitted to average age-specific body mass data of control chicks in each foster unit, and the resulting curve parameters were used to calculate the age at which the mean mass of control chicks in the respective foster unit was the same as that of an individual deprived chick at the end of deprivation. Then, the mean mass of the respective control chicks was estimated three days after they had the 7 d mass of the individual deprived chick (individual-specific control expected mass). Finally, control expected mass was compared with actual 10d mass for all deprived chicks in a paired t test. If actual 10d mass is significantly higher than control expected mass, it can be concluded that the faster growth of deprived chicks is not explained by their position on the growth curve. All probabilities reported here are two-tailed, and means are shown with their standard errors.

Results

Nestling sizes and masses at different ages generally showed higher effects of nest of origin than growth

increments, but lower effects of the rearing environment, as represented by trio (for all statistical details, see Tables 1 and 2). The impaired growth after male removal significantly reduced the originally similar body mass of chicks in widowed nests in comparison to control nests (Fig. 1A). After translocating both groups to a similar control environment at 7d of age, previously deprived chicks grew significantly faster in body mass than controls, leading to a similar body mass of treatment groups by 10d of age, with no growth difference thereafter (Fig. 1A and 2A). Moreover, the 10d mass of deprived chicks was significantly higher than that expected from the control growth curve (squared values to normalize distribution, paired $t_{72} = -2.208$, $P = 0.030$).

Tarsus length could only be measured from 7 d of age, but it showed a very different growth trajectory in relation to the experimental treatment than body mass (Fig. 1B and 2B). The 7 d tarsus length of young reared by widowed females was smaller than that of controls (Fig. 1B). In the 7–10 d post-deprivation phase, the tarsus length of previously deprived chicks grew significantly slower relative to its original size than that of control chicks, which further increased the treatment effect on tarsus length (Fig. 1B and 2B). Tarsus growth controlled for original size did not differ between the groups from 10 to 12 d of age, and the strongly reduced size of widowed chicks persisted until fledging (Fig. 1B and 2B).

Discussion

Studying developmental plasticity

The potential of food-deprived young birds to adjust their growth rates to improving environmental conditions is a controversial topic (Lepczyk and Karasov 2000). Compensatory growth acceleration has been reported in precocial, semiprecocial or semialtricial birds (Osborn and Wilson 1960, Heath and Randall

1985, Negro et al. 1994, Schew 1995), but not in the few studies on altricial species (Schew 1995, Konarzewski et al. 1996, Lepczyk and Karasov 2000). The latter studies, however, were conducted by hand-rearing the nestlings in the laboratory. They were therefore unable to mimic natural levels or contents of food in either the limited or the unlimited phase, while the switches between food regimes could be strictly controlled. Recently, Bize et al. (2003) examined developmental plasticity in a natural population of altricial alpine swifts by manipulating the loads of ever-present ectoparasites in the nests in two directions (parasitized or deparasitized). Since the parasite populations naturally declined after a certain age of the nestlings, young swifts in parasitized nests had an opportunity to reduce their growth disadvantage. Accordingly, in the late phase, both efficient catch-up growth and delayed fledging were observed (Bize et al. 2003).

Short-term, abrupt changes in food availability (due to e.g. a few rainy days) are common in nature. The effects of these on chick growth may differ from those of the gradual dynamics of nest parasite populations (McCarty and Winkler 1999). In particular, food shortages limited to specific parts of development may most seriously affect the organs which show the most pronounced growth in the respective periods (Dobbing 1981), and an allocation hierarchy may exist among the developing body parts at each age (Schew 1995). On the other hand, the timing of nutritional stress relative to fledging obviously delimits the opportunities for the nestlings to recover, because as morphological traits gain their mature functional structure towards fledging, their potential for further growth gradually diminishes (Carrier and Leon 1990, Ricklefs et al. 1994). Studies are needed which examine the given species in its natural environment, apply treatments which approximate naturally occurring levels of food stress, and accurately control the periods of food limitation. This allows a detailed quantification of age-dependent responses in the periods of limitation and compensation.

Table 1. The age-specific body mass and tarsus length in collared flycatcher chicks, in relation to food deprivation treatment (see Methods) as fixed effect, and foster unit (trio) and nest of origin (nested within trio) as random effects. *, $P < 0.05$; ***, $P < 0.001$; †, NS after Bonferroni correction.

Dependent variable	Treatment		Trio		Nest of origin	
	F (df)	Estimate (SE)	Z	Estimate (SE)	Z	Estimate (SE)
2 d mass	0.09 (1,122)	-0.22 (0.73)	0.75	2.88 (3.84)	1.63	6.46 (3.95)
4 d mass	1.77 (1,122)	-1.72 (1.29)	0.08	0.89 (11.14)	1.78*†	26.64 (15.00)
7 d mass	52.47*** (1,122)	-13.70 (1.89)	0.93	23.82 (25.65)	1.56	37.43 (23.94)
10 d mass	2.32 (1,122)	-2.77 (1.82)	1.22	30.85 (25.29)	1.46	27.56 (18.89)
12 d mass	0.17 (1,122)	-0.69 (1.70)	0.40	4.77 (11.81)	1.27	17.75 (14.00)
7 d tarsus	22.81*** (1,122)	-6.02 (1.26)	0.80	11.91 (14.83)	1.80*†	26.71 (14.88)
10 d tarsus	35.72*** (1,122)	-4.57 (0.76)	0.23	0.85 (3.69)	1.69*†	8.08 (4.78)
12 d tarsus	25.51*** (1,122)	-3.80 (0.75)	0.49	1.31 (2.67)	1.33	4.25 (3.21)

Table 2. The growth of body mass and tarsus length in collared flycatcher chicks, in relation to food deprivation treatment (see Methods) and size before the growth stage as fixed effects, and foster unit (trio) and nest of origin (nested within trio) as random effects. *, $P < 0.05$; ***, $P < 0.001$; †, NS after Bonferroni correction.

Dependent variable	Treatment		Original size		Trio		Nest of origin	
	F (df)	Estimate (SE)	F (df)	Estimate (SE)	Z	Estimate (SE)	Z	Estimate (SE)
Mass growth 4–7 d	99.08*** (1,121)	-11.61 (1.17)	5.17*† (1,121)	0.16 (0.07)	2.08*†	33.39 (16.02)	0.00	0.00 (0.00)
Mass growth 7–10 d	27.17*** (1,121)	7.22 (1.38)	28.63*** (1,121)	-0.27 (0.05)	2.15*†	53.52 (24.95)	0.00	0.00 (0.00)
Mass growth 10–12 d	2.29 (1,121)	1.40 (0.92)	35.27*** (1,121)	-0.24 (0.04)	1.03	4.91 (4.75)	1.06	4.14 (3.92)
Tarsus growth 7–10 d	12.73*** (1,121)	-2.20 (0.62)	271.10*** (1,121)	-0.61 (0.04)	1.33	3.62 (2.73)	1.35	2.56 (1.89)
Tarsus growth 10–12 d	0.01 (1,121)	-0.04 (0.42)	21.43*** (1,121)	-0.18 (0.04)	1.76*†	1.42 (0.81)	0.00	0.00 (0.00)

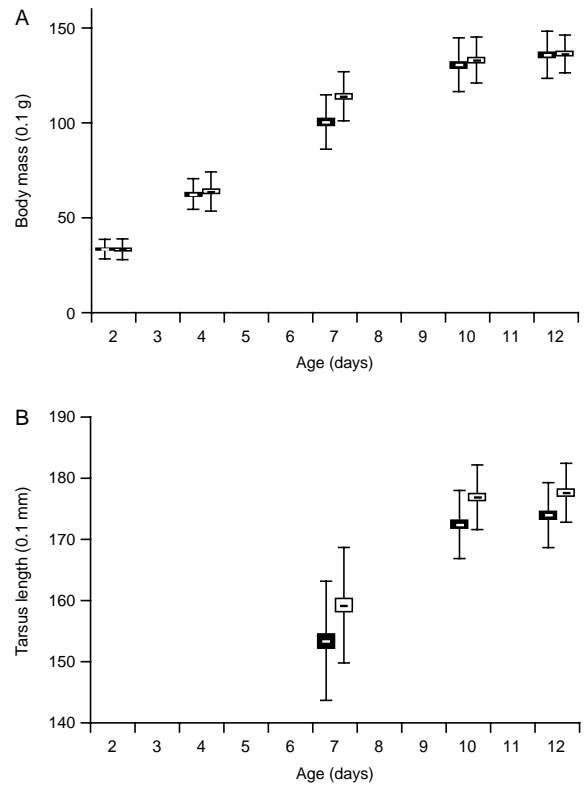


Fig. 1. The growth of (A) body mass, and (B) tarsus length in collared flycatcher chicks in relation to age and temporary food deprivation treatment; means \pm SE, SD. Filled boxes, deprived chicks; open boxes, control chicks.

Trait-specific catch-up growth in collared flycatcher chicks

The experiment presented here was aimed to restrict food scarcity to a well defined phase of the growth of collared flycatcher chicks, by removing males for a period of three days after the chicks reached the age of 4d. At 7d of age, the male at the widowed nest was released, and both groups were moved to nests with undisturbed parents, to ensure that food-restricted and control chicks would face similar rearing conditions for the rest of the nestling period. The male removal treatment was timed to the period of rapid growth, but after the food restriction ended, treated chicks still had an opportunity to compensate for their potentially smaller mass and structural size (Rosivall et al. 2005, Hegyi et al. 2006a).

Male removal strongly reduced the growth rate of body mass, and resulted in much lighter chicks in the treated relative to the control group by the age of 7 d. After the cessation of food limitation, however, the mass gain of treated chicks relative to original mass became much faster than that of controls. Moreover, a computer simulation controlling for age-independent, mass-specific position on the growth curve also indicated faster

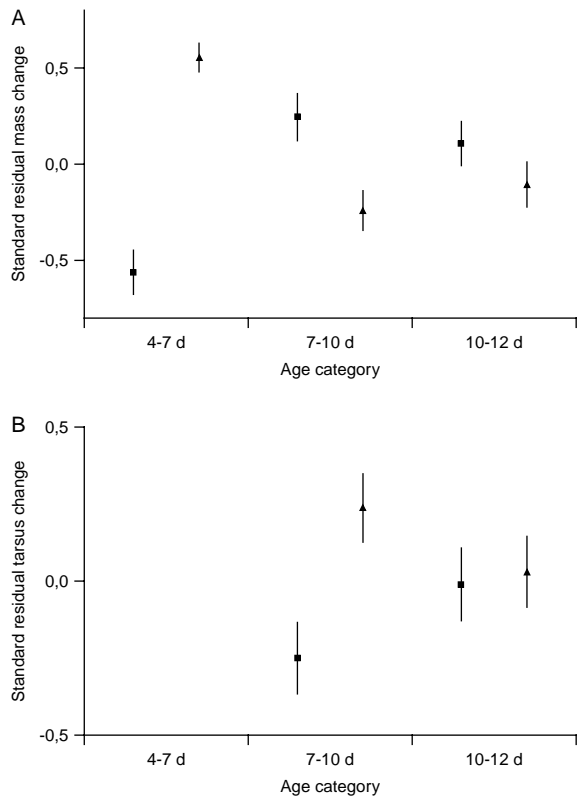


Fig. 2. Changes of (A) body mass, and (B) tarsus length in collared flycatcher chicks in relation to age and temporary food deprivation treatment; means \pm SE. Standard residuals are shown from a regression of mass/size change on mass/size before the respective developmental phase. Squares, deprived chicks; triangles, control chicks.

growth in deprived than in control chicks. From the age of 10 d, there was no difference in mass or mass growth between treated and control chicks. It can therefore be concluded that, contrary to most previous findings in altricial species (Lepczyk and Karasov 2000, but see Bize et al. 2003), the developmental plasticity of body mass in collared flycatchers extends to compensatory growth acceleration. To the authors' knowledge, this is the first report of catch-up growth in a passerine bird. The extent to which the accelerated mass growth observed here involved a gain of functional tissue or only an accumulation of fat reserves is unknown (Osborn and Wilson 1960). However, as the increased growth ended well before fledging, any additional fat could potentially be converted to internal organs before independence.

The pattern of the growth of tarsus length in relation to treatment was markedly different from that of body mass. Tarsus length can be measured reliably only from 7 d of age, so we cannot rule out the possibility that the small 7 d tarsi of young in widowed nests are due to the small genetic size of these young

or due to incidental differences in parental investment into eggs. However, small genetic size is probably not the case here, since no difference was found among treatment groups in the tarsus length of parents, and nonrandom egg investment patterns are also unlikely, since the groups did not differ in 2 d body mass, which is strongly related to egg size (Rosivall et al. 2005). We therefore suggest that the reduced 7 d size of food-limited chicks relative to controls was probably the nutritional consequence of male removal. After the translocation to a control environment, the treatment difference in the growth of tarsus length was in a surprising direction, with previously food-deprived chicks growing slower than controls, when their small 7 d size was taken into account. When 7 d tarsus was removed from the model, growth rates no longer differed between the treatments ($F_{1,122} = 2.29$, $P = 0.133$). This shows that treated chicks did not adjust their tarsus growth to the size reduction suffered in the male removal phase. From 10 to 12 d of age, both treated and control chicks grew as expected from their 10 d tarsus lengths, and initially food-deprived young were highly significantly smaller than controls at the pre-fledging measurement. It cannot be ruled out that chicks continued to grow after our last measurement, but in this final asymptotic phase, the remaining growth is not likely to have removed the large treatment effect present at 12 d of age. Because of the limited opportunity to increase tarsus length after 12 d of age, fledging dates are also unlikely to have differed between deprived and control chicks.

There are several potential explanations for the lack of catch-up growth in tarsus length. First, that skeletal size was close to its maturity, and therefore little compensation could be expected (Carrier and Leon 1990). Although tarsus growth was highly significant at both the 7–10 d and the 10–12 d age transitions (repeated measures mixed models, $P < 0.001$ in both cases), the 7 d tarsus length of chicks was on average 88.9% of their 12 d size, while the corresponding figure for body mass was only 78.9%. Another explanation is that the developmental plasticity of skeletal size is smaller than that of body mass (Negro et al. 1994, Markman et al. 2002, Dahdul and Horn 2003). These explanations, however, fail to account for the reduced tarsus growth of treated chicks relative to their original size after the removal of food stress. The 7–10 d growth reduction raises the possibility that temporarily food-deprived flycatcher young sacrificed their skeletal size and channeled the acquired energy towards mass growth in the period of compensation, in order to ensure a sufficient level of body reserves at fledging (also see Nilsson and Gårdmark 1996, Saino et al. 1998). Indeed, fledging body mass is a very important determinant of postfledging survival in this long-distance migratory species, as reflected by local

recruitment rates (Lindén et al. 1992, Török et al. 2004, own unpubl. data). However, it is possible that the slower 7–10 d tarsus growth has nothing to do with the faster mass growth in the same phase. For example, due to its smaller flexibility than body mass, skeletal size may only gradually return to its normal developmental course after the end of food restriction.

Conclusions

These results experimentally demonstrate the presence of catch-up growth in a passerine bird, and suggest that developmental plasticity differs between skeletal traits and body mass. More studies are needed to examine the way and extent of compensatory growth in various bird species. Data covering a broader taxonomic range will permit the comparative examination of ecological and evolutionary factors promoting developmental plasticity and its specific pathways, analogously to previous studies on other characteristics of the nestling growth period (reviewed by Remeš and Martin 2002). Future studies will also reveal how the timing of food restriction relative to fledging affects the compensation response through the growth-maturation trade-off (Ricklefs et al. 1998) and the developmental hierarchy of organs (Schew 1995). Finally, long-term experiments should investigate the fitness consequences of compensatory growth, for example by comparing the observed hierarchy of traits during compensation with their relative importance in determining survival and fecundity, or by assessing the short- and long-term physiological costs of developmental plasticity (Metcalf and Monaghan 2001).

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