ORIGINAL ARTICLE

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Paternal age and offspring growth: separating the intrinsic quality of young from rearing effects

Abstract Younger individuals are often less successful in reproduction than older ones. This might be because of improving breeding skills with age or because the genetic quality of young or early maternal effects on them vary with parental age. However, no attempt has been made to experimentally separate these processes in vertebrates. We conducted a cross-fostering experiment in collared flycatchers (*Ficedula albicollis*) in three breeding seasons to disentangle origin- and rearing-related effects of paternal age on chick growth, while controlling for date-specific environmental conditions as well as differences in clutch and brood size. The age of the male at the nest of origin, but not that of the rearing male, had a year-dependent effect on nestling body mass and tarsus length. In two seasons, young of subadult males grew slower in the early linear phase of growth than young of adult males. There was no compensatory growth in the final asymptotic phase, so both body mass and tarsus length before fledging reflected the differential early development. In the remaining year, the age of the male at the nest of origin had no significant effect on chick growth. The environment-dependent origin effect we detected was unexplained by incubation times, hatching asynchrony, chick masses at swapping or previously described age-dependent egg quality patterns. Our results therefore suggest a genotype × environment interaction on the relative development of offspring sired by subadult and adult males. Our results also raise the possibility that female birds may gain genetic benefits by mating with older males. Further studies should identify general patterns of male age-dependent female mate choice and offspring quality in different environmental conditions.

Communicated by M. Leonard

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Introduction

Reproductive performance is age-dependent in a variety of taxa (Clutton-Brock 1988). In insects, for example, age has been found to affect the mating success (Jones et al. 2000) and mating tactics of males (Engqvist and Sauer 2002; Kemp 2002), as well as the quality of offspring produced by females (Fox et al. 2003). In a population of sockeye salmon *Oncorhynchus nerka*, early- and late-breeding females represent genetically diverged alternative strategies with contrasting levels of investment to egg production vs survival to defend the nest (Hendry et al. 2004). In the sand lizard, *Lacerta agilis*, the growth of body size appears to largely explain age-related changes in reproductive behaviour and success in both sexes (Olsson and Shine 1996). In red deer *Cervus elaphus*, sex dependence in the relative allocation to somatic maintenance vs reproduction reflects the age dependence of reproductive prospects of males vs females (Carranza et al. 2004). Age-dependent reproduction, however, has been most thoroughly studied in birds.

The reproductive performance of birds shows a characteristic pattern across age categories. Young breeders usually raise fewer or poorer-quality young than older birds (Røskaft et al. 1983; Perrins and McCleery 1985; Lessells and Krebs 1989; Sydeman et al. 1991; Hepp and Kennamer 1993; Blomqvist et al. 1997; Hipfner and Gaston 2002), while individuals exceeding a certain age threshold often show a decline in breeding success (Ollason and Dunnet 1978; Dhondt 1989; Hamer and Furness 1991; Ratcliffe et al. 1998; Pyle et al. 2001).

Due to the unequal roles or investment of the two sexes during breeding, the age of females is more important to success than that of males in some species, such as blackbirds *Turdus merula* (Desrochers and Magrath 1993), nuthatches *Sitta europaea* (Enoksson 1993) and red-billed choughs *Pyrrhocorax pyrrhocorax* (Reid et al. 2003),

while the reverse is true in other species, for example, Tengmalm's owls *Aegolius funereus* (Korpimäki 1988), brown thornbills *Acanthiza pusilla* (Green 2001) and lapwings *Vanellus vanellus* (Parish et al. 2001). However, for historical and practical reasons, most studies focused on females.

The poor success of young parents has two distinct but not mutually exclusive classes of explanations. First, the performance of individual birds may improve with age because parenting skills improve (Brandt 1984; Desrochers 1992a; Weimerskirch 1992; Cichon 2003), or because of an increase in reproductive effort (Pugesek 1981, 1984; Pärt et al. 1992) or territory quality (Major et al. 1999; Pärt 2001a). Second, the success differences between young and old breeders may result from processes operating before or during egg production, for example, differences in genetic or long-lasting phenotypic quality of parents that cause differential survival (Nol and Smith 1987; Bradley et al. 1989; Smith 1993; Cam and Monnat 2000; Mauck et al. 2004), or male age-related differences in egg investment by females (Michl et al. 2005).

If the relationship between the age and reproductive success of parents is due to genetic quality or early maternal effects on young, we expect to find differences in offspring quality among parental age classes irrespective of the rearing environment provided by the parents (Brooks and Kemp 2001). Improving parenting skills, in contrast, will lead to differences in the rearing environment, irrespective of the genetic or long-lasting phenotypic quality of young. The few published experiments on age-related reproductive success were designed to disentangle age and experience (Pärt 1995; Cichon 2003), age and territory quality (Pärt 2001a) or breeding date and parental quality effects (Desrochers 1992b; DeForest and Gaston 1996; Daunt et al. 1999, 2001). No experimental study in any vertebrate species addressed the question of whether there are intrinsic differences in quality between the offspring of young and older parents.

A straightforward way to assess the quality of young would be to measure nestling growth. However, the overwhelming majority of studies considering nestling size or condition only reported single morphological measurements taken before fledging or independence (Naef-Daenzer et al. 2001; Tremblay et al. 2003). This is unfortunate for several reasons. First, the importance of several early environmental effects decreases towards fledging (Smith et al. 1995; Schwabl 1996), which implies that fledgling data may often lead to false negative conclusions on the importance of environmental factors to chicks. Second, there is a considerable degree of flexibility in chick growth, which may be a signature of individual quality itself (Lepczyk and Karasov 2000; Bize et al. 2003). Third, developmental fluctuations may have long-term effects on the fate of young even if they do not lead to differences in final size (Metcalfe and Monaghan 2001). Studies of chick growth in relation to parental age are rare and almost completely restricted to seabirds (e.g. Sætre et al. 1995; DeForest and Gaston 1996; Galbraith et al. 1999). In some of these studies, the results obtained for

growth vs final size were consistent with each other (Pugesek 1993; Wendeln and Becker 1999), but there was a disagreement between them in other studies (Berrow et al. 2000).

Some of the existing evidence for parental age effects come from work on Old World flycatchers. However, the majority of studies on age-related reproduction in these species have been restricted to females (e.g. Gustafsson and Pärt 1990; Pärt et al. 1992; Cichon 2003). Relatively little is known on patterns with male age. In collared flycatchers (*Ficedula albicollis*), the age of males significantly predicted seasonal reproductive success even after correcting for breeding date and female age (Qvarnström et al. 2003). However, this study focused on the costs of polygyny, and no specific details were provided on the age effect, i.e. its direction or interactions with other variables were not shown. In the sister species, the pied flycatcher (*Ficedula hypoleuca*), the chicks grew better in the broods of old, colourful males than in those of young, dull males, when the female parents were temporarily removed (Sætre et al. 1995). An earlier descriptive study by Harvey et al. (1985) showed that yearling males which subsequently survived to breed again bred earlier in the current season than those which did not survive. This pattern suggested that at least part of the variation in success between yearlings and adults could be attributed to differences in genetic or long-lasting phenotypic quality.

In this paper, we report on a cross-fostering experiment in a population of collared flycatchers where we partitioned the difference in offspring growth between the nests of subadult and adult males to rearing- vs origin-related components. The experimental design corrected for confounding date-related environmental differences between male age classes, for example, timing relative to the caterpillar availability peak (Nager and van Noordwijk 1995), and also controlled for most of the differences in territory quality, as reflected by settlement and pairing order (Alatalo et al. 1986; Pärt 1991). If genetic or egg quality effects in relation to male age are important determinants of nestling growth, we predict a significant 'male of origin' effect. If, on the other hand, male parental quality (Sundberg and Larsson 1996), female parental care (Limbourg et al. 2004) or territory quality (Pärt 2001a) in relation to male age are important, we expect to find a significant rearing effect. Both the origin and the rearing effect have several alternative explanations. To distinguish between the alternatives, we refer to previous results in our population on aspects of egg composition as early maternal effects (Hargitai et al. 2005; Michl et al. 2005) and report the feeding rates of both parents at the experimental broods.

Materials and methods

Study species and area

The collared flycatcher is a small (ca. 13 g), insectivorous, hole-nesting passerine (Gustafsson 1989). The species is

predominantly monogamous, with approximately 10% of males attracting two females (Garamszegi et al. 2004). The study was conducted in Pilis Mountains, near Szentendre, Hungary (for more information on the study area, see Török and Tóth 1988, for a review). Males arrive at our nestbox plots in the middle of April, and females a few days later. After pair formation, females build the nest, lay and incubate the eggs, while the two parents share nestling feeding approximately equally. Male participation in provisioning the brood is important to reproductive success (Garamszegi et al. 2004). The median clutch size is six (range 2–9). The incubation period is 12–13 days, and the nestlings fledge from 14 days after hatch. Males show delayed plumage maturation, with second-year (subadult) males having brown remiges and a small white wing patch and older males (adults) having black remiges and a much larger wing patch (Török et al. 2003). Subadult males constitute approximately 30% of the breeding population each year (mean±SE from 1990 to 2004, 0.298±0.036). Both the body mass and the tarsus length of fledglings show positive linear relationships with recruitment probability (J. Török et al., unpublished data; also see Lindén et al. 1992; Török et al. 2004, for a review).

Experimental procedures

The experiment was done in the breeding seasons of 2002 to 2004. We presented dummy males at all nests on the experimental plots during the late nest building or early egg laying period and observed the attacking resident with binoculars. The age of the resident male (subadult or adult) was determined by the colour of the remiges (Svensson 1992) and wing patch size (Török et al. 2003). The nests were monitored daily around the expected date of hatching. We identified trios consisting of the nests of one subadult and two adult males, matched for hatch date and brood size. Two days after hatching, we swapped the whole broods in these trios of nests, creating three experimental foster categories: subadult males rearing offspring of adult males (SMAO), adult males rearing offspring of subadult males (AMSO) and adult males rearing offspring of adult males (AMAO). Our basic question was whether differences in nestling development between the paternal age classes were due to different rearing environments or origin-related effects. The number of nests tended by subadult males was insufficient for a second control group, with subadult males and subadult offspring, which would be needed to test the interaction between origin and rearing effects. However, because we did not detect a rearing effect in any year of this study (see "Results"), adding a second control group would have been unlikely to have revealed more complex patterns. To see whether differential incubation confounded the origin effect (Gorman and Nager 2004), we compared incubation times across treatment groups. Incubation time was defined as the time between the laying of the sixth egg and hatching.

The number of trios swapped was 8 in 2002, 9 in 2003 and 12 in 2004, involving a total of 87 nests. Eight trios were dropped from the data set because of predation ($n=3$ in 2002; $n=1$ in 2003), misidentification of male age ($n=1$ in each year) or lack of a male parent ($n=1$ in 2004). One male was detected in the same experimental treatment in 2 years, and we omitted its second observation from the analyses. Five females also occurred twice, in the same ($n=2$) or different experimental treatments ($n=3$), which necessitated the statistical control of female identity. One experimental nest in each year was identified as polygynous secondary based on laying date and male identity, all belonging to the AMSO category. As it was confirmed that these males fed the young and omitting the three trios including their nests did not affect the conclusions, we retained them in the analyses but statistically corrected for their presence. The analyses presented here are thus based on a sample of 20 trios (four in 2002, seven in 2003 and nine in 2004), with a total of 60 nests.

In 2002 and 2003, the feeding rates by the parents were recorded by video cameras in 1-h sessions when broods were 4 days old. The recordings of a given trio were run at the same time, with a maximum difference of 45 min. All young received standard numbered aluminium rings at the age of 6 days. Body mass was measured to the nearest 0.1 g with a Pesola spring balance every other day from the day of swapping to the age of 12d. Tarsus length was measured with a caliper to the nearest 0.1 mm at the age of 8, 10 and 12 days. Nestlings are usually considered fully grown at the age of 13 days. We captured the parents in the nestbox when chicks were 8 to 10 days of age and measured their body mass, tarsus length and white plumage ornaments (forehead patch size, Hegyi et al. 2006; wing patch size, Török et al. 2003).

Statistical analyses

To simplify the models and to facilitate the interpretation of the results, we pooled data from 2002 and 2004 and compared them with 2003 as a separate group. In this case, we show the results using these 2-year categories. Preliminary analyses with year as a factor showed four significant or marginal year by male of origin interactions on nestling development. In pairwise tests between years, all of the 4 year × origin interactions were far from significance for 2002 and 2004, while seven of the eight were significant or marginal for 2003 and the other 2 years. As mass gain was steeper and levelled off earlier in 2003 than in 2002 or 2004 (see "Results"), 2003 was termed 'good year', while 2002 and 2004 were 'average years'.

Growth measurements of nestlings that died in the nest were dropped from the analyses. Mortality was rare (one chick in $n=8$ nests and two chicks in $n=3$ nests), and all except one of the nestlings that died were runts originating from pronounced hatching asynchrony. The number of nests with dead nestlings did not differ among year types (6 of 39 nests in average years and 5 of 21 nests in the good year; Fisher exact $p=0.493$) or treatments (1 of 20 SMAO nests, 3 of 20 AMSO nests, and 7 of 20 AMAO nests; Fisher exact tests SMAO–AMSO $p=0.605$, SMAO–

AMAO $p=0.043$, and AMSO–AMAO $p=0.273$; all ns after Bonferroni correction). However, as nestling mortality may enhance the growth of the remaining young, we tried to correct for the small difference by entering mortality into the analyses of growth in two ways: as a binary factor and as a continuous covariate (the number of dead nestlings). The main effect of mortality was nonsignificant in all cases (all $p>0.12$), and the results remained almost quantitatively identical, with no loss or gain of significance. It seems, therefore, that mortality did not confound the nestling growth patterns in our case. We therefore excluded mortality from the models presented here.

Hatching asynchrony may cause growth retardation in late-hatched nestlings, which may influence the brood-level growth data. We did not directly follow the patterns of hatching in the experimental nests. However, hatching asynchrony obviously affects size variation within broods after hatching (E. Szöllősi et al., unpublished data). We therefore calculated the within-brood standard deviations of 2-day chick masses and compared them among treatment groups (see "Results"). In addition to male age, some of the male and female traits we measured differed among treatments (Table 1). However, when adding these traits one by one to the models, most had no significant effect (only 1 significance in 27 models), and none affected any of our conclusions, so we removed them from the models.

Male and female feeding rates were expressed as feedings per nestling per hour. Nestling growth rates were assessed in two phases. For the early, linear phase, only mass data were available. We calculated the slope of regression lines of brood means from 4 to 8 days of age. For the late decreasing phase of growth, both mass and tarsus growth were quantified by two variables: changes from 8 to 10 days and from 10 to 12 days, with original size measures (i.e. 8- and 10-day mass or tarsus, respectively) entered as covariates. Entering original size as a covariate

is an attempt to correct for the decline of growth: the larger the nestling, the smaller the remaining growth (also see "Results"). This also implies that late growth rates are deviations from the growth expected with the current size. Mass and tarsus growth rates for the 8- to 10-day and 10- to 12-day periods were only weakly correlated (mixed models with female and trio as random factors, changes corrected for original mass or tarsus; mass $F_{1, 53.9}=1.82$, $p=0.182$; tarsus $F_{1, 53.8}=4.41$, $p=0.040$), so they were treated separately.

To control for the occurrence of polygyny (see above), we entered it as a binary factor into the analyses. We used general linear mixed models with Satterthwaite correction, calculated in the MIXED procedure of SAS 8.02 (SAS Institute). We treated brood means as data points, year type, age of the male of origin (hereafter: origin), age of the male of rearing (hereafter rearing) and polygyny as fixed factors, and trio and female as random factors. Backward stepwise model selection was applied in all tests. As we used three measures of mass and two measures of tarsus growth, we corrected the critical p to 0.05/3 and 0.05/2, respectively, in the statistical tests of these variables.

Results

Potential background variables and confounds

Neither incubation times nor body mass of nestlings at swapping or brood-level standard deviations of 2-day mass differed across treatments (Table 2). There was no indication of differential feeding by males in relation to male age treatments. Females, in contrast, showed reduced feeding rates when paired to subadult males (significant rearing effect; Table 2, Fig. 1). None of the patterns of incubation times, original chick masses, their standard deviations or

Table 1 Comparison of morphology and ornamentation of males and females among treatments and year types

	Year type		Treatment		Interaction	
	df	F	df	F	df	F
Female tarsus	1, 19.1	7.92*	2, 34.3	0.54	2, 29.7	3.79*
Female mass	1, 2.27	0.42	2, 9.55	1.83	2, 6.46	6.32*
Female condition[a]	1, 2.79	0.29	2, 1	1.14	2, 3.12	1.61
Female wing patch size	1, 16.3	1.66	2, 35.1	0.96	2, 35.2	3.10
Female minimum age[b]	1, 15.6	0.86	2, 31.2	0.14	2, 27.5	1.39
Male tarsus	1, 18	1.44	2, 34.2	1.92	2, 34.2	0.84
Male mass	1, 5	0.18	2, 5	1.39	2, 5	0.23
Male condition[a]	1, 48	0.30	2, 48	1.47	2, 48	0.42
Male forehead patch size	1, 52	0.00	2, 52	3.05	2, 52	0.07
Male wing patch size[c]	1, 33	4.90*	1, 33	0.19	1, 33	4.57*
Male minimum age[bc]	1, 34	0.14	1, 34	0.00	1, 34	0.62

Linear mixed models with year type and treatment (three groups) as fixed factors and trio and female as random factors
*$p<0.05$; **$p<0.01$
[a]Body condition values are residuals from a regression of tarsus length on body weight
[b]Log (2) transformed. Female age was known for recruits and estimated as 1 year at first capture for an unringed adult. For male age determination, see Török et al. (2003), for a review
[c]Only the adult males are compared here, because subadult males have very small wing patches and their age is obvious

Table 2 Relationship of male age at the nest of origin ('origin') and rearing ('rearing') and year type with incubation time, chick mass at 2 days of age, the standard deviation of mass at 2 days of age, parental feeding rates at 4 days of age, the mass and tarsus growth rates of chicks in different phases and their mass and tarsus length before fledging

	Year type		Origin		Year type* origin		Rearing		Year type* rearing	
	df	F	df	F	df	F	df	F	df	F
Incubation time	1, 14.7	5.12*	1, 34.9	2.56	1, 33.9	0.94	1, 32.5	0.36	1, 32.7	0.08
2-day mass	1, 18.2	0.38	1, 38.1	0.07	1, 37.4	2.68	1, 36.6	2.37	1, 35.6	0.01
2-day mass SD	1, 14.8	1.41	1, 33.3	0.60	1, 18.9	2.43	1, 12.6	1.16	1, 16.5	0.12
Male feeding rate	1, 26	2.46	1, 26	0.04	1, 24	0.33	1, 26	0.48	1, 24	0.24
Female feeding rate	1, 10.5	4.14	1, 9.85	1.25	1, 3.57	0.25	1, 9.23	8.16*	1, 4.29	1.40
Mass growth 4–8 days[a]	1, 51	32.47***	1, 51	1.35	1, 51	8.98**	1, 5	0.30	1, 49	0.14
Mass growth 8–10 days	1, 22.2	20.82***	1, 36.7	0.15	1, 38	4.41*[b]	1, 31.6	0.11	1, 31.2	1.47
Mass growth 10–12 days	1, 17.7	0.01	1, 37	0.01	1, 37.2	0.83	1, 34.9	0.40	1, 33.7	0.11
Tarsus growth 8–10 days[a]	1, 14.7	1.31	1, 33.5	0.10	1, 35.4	2.17	1, 32	1.96	1, 31.2	1.83
Tarsus growth 10–12 days[a]	1, 17.3	1.93	1, 34.3	0.36	1, 35.2	0.41	1, 33.2	0.48	1, 33.1	0.10
8-day tarsus[a]	1, 14.5	2.57	1, 36.9	0.83	1, 39.5	17.67***	1, 39.8	0.12	1, 39.8	0.76
12-day mass	1, 13.4	0.03	1, 34.6	1.08	1, 26.4	5.00*	1, 20.1	0.10	1, 13.7	0.06
12-day tarsus	1, 15.3	2.44	1, 34.2	0.83	1, 33.6	7.64**	1, 30.5	0.00	1, 46	0.03

Linear mixed models, see "Materials and methods" for details

*$p<0.05$; **$p<0.01$; ***$p<0.001$

[a]Significant effect of polygyny

[b]Not significant after Bonferroni correction

parental feeding rates with treatment was influenced by environmental conditions, as reflected by the interactions between treatments and year type (Table 2).

Experimental analysis of nestling growth rates

There was no overall origin effect on the 12-day mass or the tarsus length of nestlings, and the growth of these traits also showed only weak effects (Table 2). There was, however, a significant year type by origin interaction for mass growth in the linear phase and from 8 to 10 days of age. Tarsus length at 8 days of age, as well as prefledging mass and tarsus values, also showed a similar interaction. Tarsus growth in the whole asymptotic phase, as well as 10- to 12-day mass growth, followed the trajectory
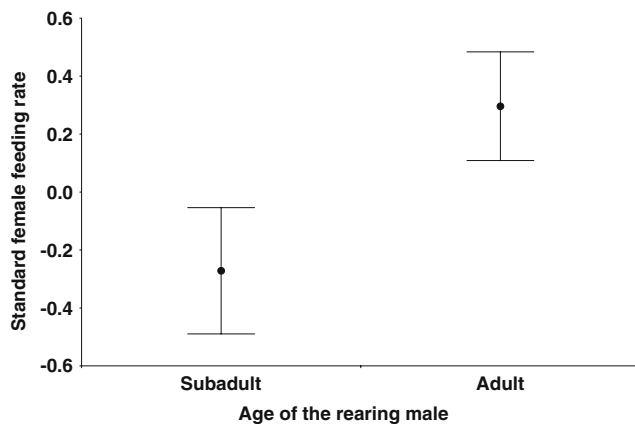
Fig. 1 Feeding rates of female collared flycatchers in relation to the age of the rearing male. Feeding rates are expressed per nestling per hour and standardized for trio (mean=0 and SD=1 for each trio)

expected from original mass or size, with no treatment effect or interaction (Table 2). Rearing had neither effect on growth nor interaction with year type (Table 2). Restricting the analysis to year types showed no significant origin effect on any trait in the good year (Table 3, Fig. 2). In the average years, however, there were significant differences related to origin for all variables showing year type by origin interactions, except 8- to 10-day mass growth (Table 3, Fig. 2). The early mass gain was poor among young of subadult males (hereafter YSM), which lead to a low mass at 8 days of age relative to young of adult males (hereafter YAM) (Fig. 2). The origin-related growth difference disappeared after 8 days of age, but the mass disadvantage of YSM was still present before fledging. Tarsus length could only be measured from 8 days of age. The 8-day tarsus length of YSM was significantly smaller than that of YAM, which suggests a slower growth in the early phase (Table 3, Fig. 2). The size difference between YSM and YAM persisted throughout the rest of the nestling period. Nestlings of subadult males reached a considerably smaller tarsus length before fledging than those of adult males.

Discussion

Experimental design and confounding factors

We have presented results from an experiment aimed to separate the origin- and rearing-related components of the relationship between nestling quality and paternal age. The high breeding density of the study population (similar to that observed in unmanaged forests; van Balen et al. 1982; Török and Tóth 1988) and the synchronous breeding

Table 3 Effect of the age of male at the nest of origin in the 2-year types on the offspring traits that showed significant year type by origin interactions

	Good year		Average years	
	df	F	df	F
Mass growth 4–8 days[a]	1, 11.4	4.74	1, 21.6	5.17*
Mass growth 8–10 days	1, 16	2.46	1, 24.7	0.16
8-day tarsus[a]	1, 11	0.51	1, 23	12.09**
12-day mass[a]	1, 17	0.73	1, 23.5	8.50**
12-day tarsus[a]	1, 17	0.71	1, 20.3	12.27**

Linear mixed models, see "Materials and methods" for details
*$p<0.05$; **$p<0.01$; ***$p<0.001$
[a]Effect of polygyny significant in average years (ns for all variables in the good year)

season of this long-distance migratory species allowed us to foster broods among trios of nests with different male age but with the same hatching date and brood size. This design made it possible to control for date-related environmental factors. Male morphology, age differences between the adult males, female age or female morphology apparently did not confound our conclusions (see "Materials and methods"). The experiment allowed, on one hand, a comparison between chicks of similar origin, reared by males of different age. A significant effect of male age in this treatment pair would suggest that male parental quality or investment, female parental investment or territory quality were responsible for male age-dependent nestling growth. On the other hand, the comparison between chicks sired by males of different age but reared in similar environments largely excludes these phenotypic effects and reflects either genetic or early maternal effects. We detected no rearing-related effect but significant year type by origin interactions.

It could be argued that including only surviving chicks in the analysis reduced variance and obscured the treatment effect. The few cases of chick mortality were almost exclusively due to late hatching and probably did not confound our results (see "Materials and methods").
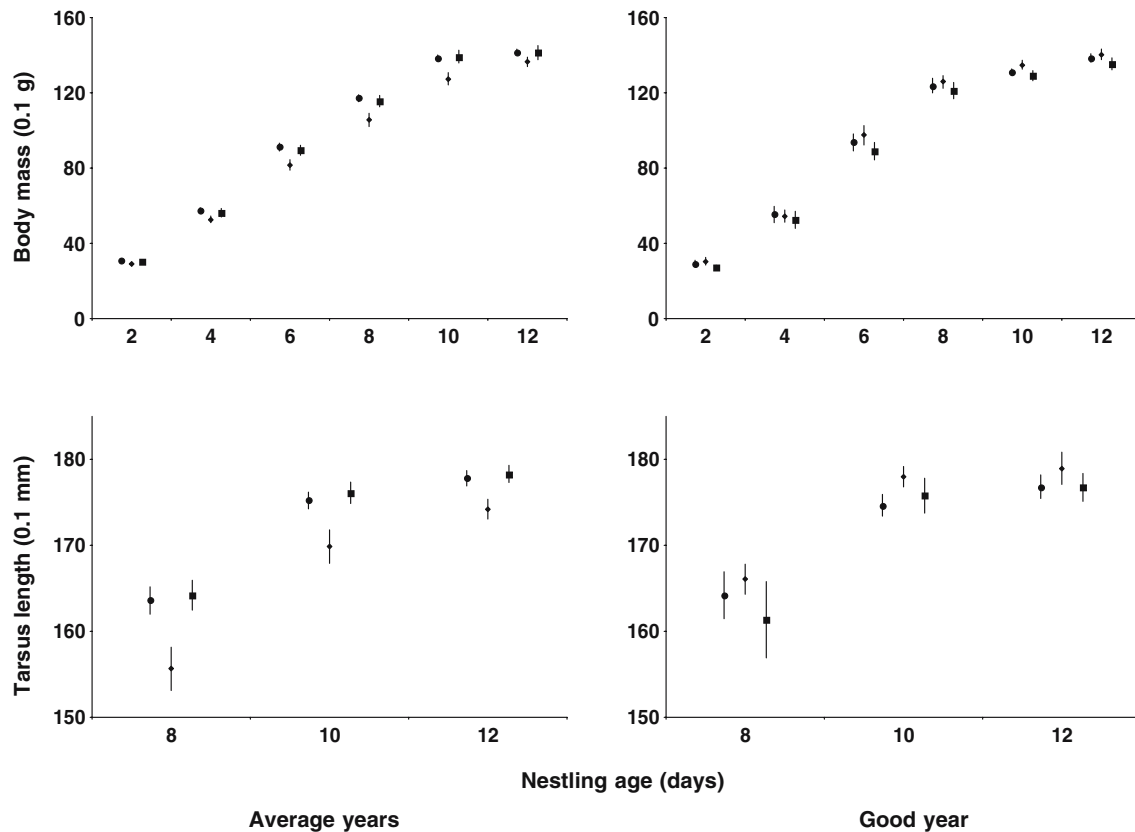
Fig. 2 Age-specific body masses and tarsus lengths (means±SE) of collared flycatcher chicks in relation to year type and treatment. *Circles*, subadult males rearing young of adult males; *diamonds*, adult males rearing young of subadult males; *squares*, adult males rearing young of adult males

Moreover, the similarity of treatment groups in within-brood mass variation at swapping suggests that the patterns of growth we detected among nests were not influenced by hatching asynchrony. Laying date may represent another source of bias. The first subadult males arrive on average later than adults, and this is reflected by the date of laying (Gustafsson 1989; Potti 1998). However, there was an almost complete overlap between the breeding dates of the two age categories in the study years. If either phenotypic or genetic quality of males was correlated with their arrival and/or mating order, cross-fostering took place between subadult males of relatively high quality and adult males of relatively poor quality. This makes our conclusions regarding genetic or parental quality conservative. In light of this, any rearing effect we detect should be viewed with caution.

Rearing effect

We found no difference in growth between young reared by subadult vs adult males. The possible differences in territory quality or parental feeding rates need to be considered when interpreting this result. Observations and experiments on site fidelity and settlement patterns of collared flycatchers indicate a learning process during which birds take the success of their own breeding attempt and that of their neighbours into account in future breeding attempts (Doligez et al. 1999, 2002). In contrast to adults, young and necessarily inexperienced males may lack the ability to discriminate between good and poor breeding sites, so that settlement order may not reflect territory quality differences in this age class (Pärt 2001b). This process may lead to differences in the quality of breeding sites even in our present comparisons between synchronously breeding pairs of subadult and adult males. However, it is possible that the feeding activity of parents compensated for the differences in territory quality. Feeding rates provide a reliable measure of energy expenditure and parental investment in our study species (Pärt et al. 1992). There was no age-related feeding by males, and females paired to adult males fed more frequently than those mated to subadult males, which may indicate preferential investment in the breeding attempt with an old, presumably high-quality male (Limbourg et al. 2004). The feeding pattern indicates that the nonsignificant rearing effect is not due to additional feeding effort by the mates of subadult males as a compensation for the poor parental performance of the male or a compensatory feeding by any member of the pair in response to the low quality of the territory. It has to be noted that we cannot rule out male age differences in the quality of prey collected (Siikamäki et al. 1998). However, to explain why the feeding pattern of females lead to no rearing effect on nestling development would require higher- rather than lower-quality food brought by subadult males in comparison to adults.

Our main conclusion is therefore that there is little evidence for lower parental or territory quality of subadult males in our population. The only comparable study was conducted in a Norwegian population of the sister species pied flycatcher, where females prefer old males with contrasting coloration to young, dull males (Sætre et al. 1994). In a female removal experiment, even the short-term growth of chicks showed a significant effect of male age, with young reared by subadult males growing slower than those of adult males (Sætre et al. 1995). At first sight, this result suggests differences in parental or territory quality between male age classes. However, the experiment of Sætre et al. (1995) did not control for the potential intrinsic differences in the quality of young reared, which may thus provide an alternative explanation to their results. The fact that the pattern was only found in the absence of the female implies that it was either due to the poor parental quality of yearling males, compensated for in the presence of females, or due to quality differences between chicks, only revealed under stressful food conditions.

Origin effect

The most important result of our study is the year-type-specific difference in the development of young of subadult vs adult males when both groups were reared by synchronously breeding adult males. Chick mass at swapping did not differ between treatments. The similarity of original mass is unlikely to reflect the balance of poor offspring quality and compensatory female investment, as females in our population were found to deposit macro-nutrients in the eggs at the same level irrespective of male age (Hargitai et al. 2005). In the average years of our experiment, young of subadult males showed a poor early growth and no late compensatory growth and therefore ended up smaller and lighter than young of adult males. This 'male of origin' effect was absent in the good year. Small body size may limit fasting endurance during the critical postfledging period (Weathers and Sullivan 1989; Merilä and Wiggins 1997) and thus affect survival, in concert with fledging mass (Lindén et al. 1992). Thus, YSM may have poor survival prospects compared to YAM in average years.

Although some of the measured female traits differed among treatment groups, the origin effect was not likely the result of female quality differences (including female age; see "Materials and methods"). The pattern could still be confounded by differential incubation by females (Gorman and Nager 2004) or differential egg investment which promotes postembryonic growth (Schwabl 1996; Lipar and Ketterson 2002). There was no difference in the length of the incubation period or in hatching success between the groups. Egg macronutrients, as reflected by egg size, similarly did not vary with male age in a very large sample of broods from our population (Hargitai et al. 2005). Moreover, females of subadult males tended to lay eggs with higher yolk volumes, which is opposite to the difference in nestling development that we detected (Michl et al. 2005). Finally, females in our population deposited more steroid into eggs if paired to subadult males

than if paired to adult males (Michl et al. 2005), again suggesting that maternal effects may reduce rather than explain the origin effects we found.

Another explanation for the male age effect on nestling growth would be a year-specific sex ratio bias in relation to paternal age, accompanied by sex-specific growth trajectories. We cannot completely exclude this possibility, but brood sex ratio was unrelated to male age in a study of this population conducted in 2002, one of the average years of our experiment (Rosivall et al. 2004). In conclusion, the patterns of incubation, egg investment and sex ratio do not seem to explain the poor early growth of YSM. The fact that the growth disadvantage of YSM was present only in average years may be due to the increased importance of genetic quality in limiting environmental conditions (David et al. 2000). The compensatory steroid investment by females (Michl et al. 2005) may also have alternatively contributed to the lack of growth difference according to 'male of origin' in the good year.

Male age and genetic quality?

Our results are consistent with the notion that the offspring of subadult males are genetically inferior compared to those of adult males. The resulting growth difference was not offset by any late compensatory growth in average years, but it was completely absent in a good year. None of the male traits we measured explained the origin effect, which implies that other unmeasured age-related determinants of male quality (for example, immunocompetence; Fair et al. 1999) may have caused the pattern. A genetic quality difference between subadult and adult males is controversial at first sight, as any subadult male is expected to become an adult male soon. However, several different approaches have shown that survival after the first breeding attempt may not be random with respect to individual quality. For example, in a Swedish population of marsh tits (*Parus palustris*), first-year laying date and subsequent survival of females were negatively correlated, and there was no within-individual advancement in laying date. Thus, the observed 'improvement' of laying date among age categories was entirely the result of selection (Smith 1993). In Leach's storm petrels (*Oceanodroma leucorhoa*), Mauck et al. (2004) found a positive correlation between the early breeding performance and longevity of individuals. Finally, in willow warblers (*Phylloscopus trochilus*; Gil et al. 2001) and collared flycatchers (Török et al. 2003), there were age-related differences in condition-dependent, sexually selected male traits among but not within individuals, suggesting viability selection for high genetic quality at certain age transitions. In our case, the relationship between male age and genetic quality may be complicated by the fact that probably not all males breed in their first year of life, as judged from the low number of subadult breeders. It is impossible, however, to separate nonbreeding males from those breeding outside our study plots. Breeding outside the plots may occur because of either problems with habitat assessment (Pärt 2001b) or

subordinance in territorial competition (Slagsvold and Sætre 1991). In any case, the most probable outcome would be that only males of high quality breed as subadults on our plots, and these sire high-quality young, a pattern opposite to that found in the present study.

Brooks and Kemp (2001) reviewed theoretical and empirical studies on age-related mate choice and offspring quality and came to the surprising conclusion that the only experiments suggesting a relationship between paternal age and genetic advantages to offspring came from insects (e.g. Price and Hansen 1998; Jones et al. 2000). This statement holds to the present day, with our study being the first attempt to investigate intrinsic offspring quality in relation to male age in a vertebrate. A link between male age and offspring quality has important implications for studies of nonrandom mating by females in relation to partner age. Evidence from several bird species indicates that females are reluctant to mate with young males. This seems to generally apply to social mate choice (e.g. Komers and Dhindsa 1989; Enstrom 1993; Sorenson and Derrickson 1994), which is easily explained by direct benefits such as parental or territory quality (see "Introduction"). The results for extra-pair mating in relation to male age are equivocal, with clear preference in some species (Wetton et al. 1995; Richardson and Burke 1999; Dickinson 2001; Karubian 2002) but apparently no preference in others (Stutchbury et al. 1997; Yezerinac and Weatherhead 1997; Krokene et al. 1998; Veiga and Boto 2000). Nonrandom extra-pair mating only rarely confers direct benefits to females (Gray 1997) and is frequently explained by the genetic quality of extra-pair young (Kempenaers et al. 1997; Sheldon et al. 1997).

Our results suggest that the choice of an adult as compared to a subadult mate in either a social or an extra-pair context may confer genetic benefits such that their offspring grow better in average food conditions, but these benefits may not be apparent in a favourable environment. Whether females use male age as a mate choice cue is unclear. No study investigated social mate choice in relation to male age in the collared flycatcher, but in the sister species pied flycatcher Sætre et al. (1994) detected significant preference for an ornament very closely related to age. In a single-year study, Sheldon and Ellegren (1999) showed no effect of male age on extra-pair paternity, but more data are needed to clarify this point. Studies that explore the relationships between male age, mating preferences and offspring quality in a range of environmental conditions are required. Further investigations should also explore the physiological mechanism behind the parental age–offspring quality relationship.

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