

Life-history consequences of growth rate depression: an experimental study on carrion crows (*Corvus corone corone* L.)

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Abstract. It has often been proposed that parents could vary the growth rates of nestling birds as an adaptive strategy to maximize reproductive output. Although it has been recognized that a depression of growth rate may result in prolonged nestling times and hence increase the probability of predation, it is often assumed that there is no phenotype-related cost of slow growth. In the present study, we assess the effect of reduced growth rates on body size and on social status of carrion crows (*Corvus corone corone* L.).

Daily weight gain for a group of nestlings was experimentally limited and a control group of siblings and non-siblings was raised under conditions of unlimited food. The growth of body mass and of linear body dimension, fledgling mass and fledgling size were compared for the two groups. Growth forms of the two groups are compared with three proposed growth models. Finally, the relation of social status of these individuals as juveniles to their former feeding group was examined.

Nestlings growing with limited food and thus with depressed growth rates reached a significantly lower final weight and reached it later than did birds fed *ad libitum*. Growth in linear body dimension followed a different pattern; nestlings with depressed growth rates reached a significantly lower tarsus length, but reached it nearly as fast as chicks with unlimited food. As juveniles, the birds of the former experimental group suffered lower social status than the control birds.

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Both sibling and non-sibling interactions resulted in significantly more wins for control birds. Our results show that the reduction of daily weight gain can affect the phenotype and fitness correlated parameters.

Key-words: Body size, *Corvus corone c.*, dominance, fitness, growth rate, life history

Introduction

Intraspecific, non-genetic variation in growth rate of nestling birds is widely observed in nature and can be attributed to a variety of causes such as habitat (e.g. Harris, 1978; Ricklefs & Peters, 1979; Ross, 1980; Richner, 1989a), season (Ricklefs & Peters, 1979; Ross, 1980), food abundance (Lack & Lack, 1951; Van Balen, 1973; Bryant, 1975, 1978; Price, 1985; Quinney, Hessel & Ankney, 1986), poor quality diet (Perrins, 1976; Boag, 1987), degree of hatching synchrony (Bortolotti, 1986), brood size (Klomp, 1970), parental age or experience. Lack (1968) proposed that parent birds may control the growth rate of their offspring in order to maximize reproductive output. That is, parents could, within their daily foraging capacity, choose to raise a small number of fast-growing chicks or a higher number of slower growing chicks. Whether growth rate reduction is caused by environmental conditions or is the effect of an adaptive parental strategy to reduce daily investment per individual chick (Drent & Daan, 1980), it is important to know at what cost growth rates can be reduced. As pointed out by Lack (1968), one cost of growing at a reduced rate is a higher probability of predation due to prolonged nestling times. Are there other costs?

To formalize the problem of costs in relation to growth, we present three different models that express the possible growth forms under depression of the instantaneous growth rate (Fig. 1). The growth constant k of the logistic equation is used to describe the rate at which the asymptotic size (a) is reached. The constant k is inversely related to the time taken to grow from hatching to fledgling size. In model 'a' the nestlings with

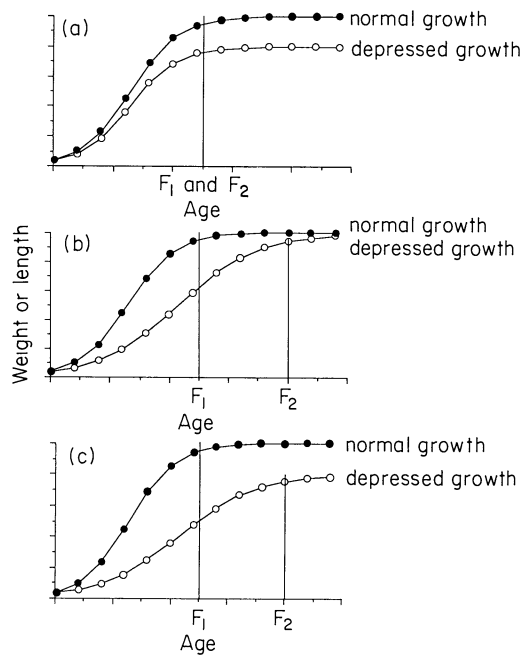


Fig. 1. Growth under depression of instantaneous growth rate may take three forms: MODEL a: Nestlings under depression of instantaneous growth rate grow with the same growth constant (k) towards a lower asymptote. MODEL b: Nestlings under depression of instantaneous growth rate grow with a lower growth constant (k) towards the same asymptote. MODEL c: Nestlings under depression of instantaneous growth rate grow with a lower growth constant (k) towards a lower asymptote. F_1 gives age of fledging of nestlings under depression of instantaneous growth rate, F_2 of fledglings under depression of instantaneous growth rate, assuming, for example, that a nestling can fledge once it reaches 95% of its asymptotic weight or size.

depressed growth rate grow with the same growth constant (k) towards a lower asymptote (a), in model 'b', the nestlings with depressed growth rate grow with a lower growth constant towards the same asymptote and finally in model 'c', which shows the combined effects of models a and b, these nestlings grow with a lower growth constant towards a lower asymptote. In model b the slow-growing birds may suffer higher predation caused by the longer nestling period. But in model a, where nestling periods are of equal length, a different cost arises if a small body size has lifetime fitness consequences for the individual, e.g. if final size determines social status and resource holding potential. In model c both costs are present.

We distinguish between the growth of body weight and the growth of linear body dimension (skeletal measurements). This is for two reasons:

first there is *a priori* no reason to believe that an increase in body weight and the growth of bones are both under the control of the same growth-regulating factors and that they therefore follow a similar growth form. Within the constraints of fine-tuned hormonal and physiological interactions during bone growth, a hypothetical growth factor, controlled by activation-repression cycles of structural and regulatory genes, may be present only for a relatively fixed time in a nestlings body. In this case the linear body size reached at the point when this growth factor is switched off would represent the final body size of a bird (Fig. 1, model a or c). Growth of body weight may follow a different pattern and, partly because of the possibility of fat accumulation, increase over a more extended time period.

Second, after fledging, selection can act independently on weight and linear body size. Postfledging survival and winter mortality of juveniles may be determined more by weight (Perrins, 1965, 1980; Howe, 1976, 1979; Fiala, 1981; Garnett, 1981), whereas factors associated with reproductive success, e.g. territory or mate acquisition, might be correlated with linear body dimension as shown by Alatalo & Lundberg (1986) in a study on pied flycatcher, *Ficedula hypoleuca* Pallas. Juvenile survival may thus correlate with fledging weight, and reproductive success or social status with linear body size. In field studies on carrion crows dominance ranking was found to be correlated with tarsus length (Richner, 1989c), and the acquisition of a breeding territory, depended also on tarsus length (Richner, 1989a).

Here we report the results of an experimental study in which we lowered growth rates in a group of carrion crow chicks by controlling food quantity, and compared growth forms, final body mass, body size, and dominance rank with those of a control group of fast-growing siblings and non-siblings. We document the growth of body weight and tarsus length to test the proposed models (Fig. 1), and evaluate the consequences of nestling growth differences on social status.

Materials and methods

Animals

We collected six broods of carrion crow chicks from an agricultural habitat in south-western Switzerland between the 10–21 May 1986. The age at the time of collection was known, and varied between 5 and 11 days. The nestlings were taken into the laboratory and individually marked,

weighed, and measured. Tarsus length was measured by bending the foot at the intertarsal joint and toes, and measuring the distance between the extreme bending points. This measure is greater than the true tarsus but is subject to a lower measurement error, especially in young chicks. Tarsus length, shown in a field study on the same species (Richner, 1989a) to be stable after fledging and to be highly correlated with other body measurements, was taken as a representative measurement of overall body size.

Experimental design

The individuals within each family were assigned to either the experimental (E) or the control (C) group, the oldest chick being randomly placed in the E- or C-group and the other chicks placed alternately in one group or the other in descending order of age.

Each bird was placed in a separate unit inside a temperature-controlled box of 1 m × 1 m × 0.7 m. The temperature was kept constant between 32°C and 34°C. Once the chicks had grown their body plumage they were transferred to a room at 20°C. Nestlings of the C-group were fed *ad libitum* at least once per hour. Chicks of the E-group were fed every hour but with a reduced quantity, which was empirically adjusted to limit daily increase of body weight to resemble that recorded for chicks in a poor urban habitat, as documented in a field study (Richner, 1989a). The weight and tarsus length were measured daily before first feeding. The food consisted of a mixture of ground beef, heart, liver, dried insects, live crickets, carrots, snail shells and a vitamin supplement. At the age of 50 days, the birds were sexed by laparoscopy (Richner, 1989b) and transferred to an outdoor aviary, where food was provided *ad libitum* for the whole group. Birds were weighed and measured again in October and December.

Curve fitting procedure

The logistic equation was used to model the tarsus growth of the chicks:

$$y = a / (1 + b \cdot \exp[-kT])$$

where y is tarsus length, T is time, a is the asymptote, k is the rate constant of the logistic equation and b is the constant of integration that translates individuals to a common time scale. The values of the parameters a , b and k were computed using an iterative least-squares fitting procedure. The parameter b is not relevant in the context of

our study and is disregarded in the analysis. Curves were fitted to the daily tarsus measurements of each chick, and then the growth parameters for the birds of the E- and C-group compared using traditional statistics (Ricklefs, 1983). The time required to grow from 10% to 90% of the asymptote as proposed by Ricklefs (1967, 1968) and adopted in many other studies was not practicable for the tarsus since the chicks reached 10% of fledging tarsus length prior to hatching. The time taken to reach 90% of final tarsus ($T_{90\%}$) length after hatching was used instead. Unlike the parameters of the growth equation, this is independent of the quality of fit of a curve to the data. Unless stated otherwise, all significance values throughout the paper are two-tailed. Since weight gain was the controlled variable, no logistic equations were fitted to the daily body weights.

Assessment of dominance

Between October and December the birds were observed for a total of 87 hours and the outcome of disputes between individuals were recorded. Dominance relationships were analysed within a group composed of the three families that numbered at least three siblings in autumn. This group consisted of six males and three females. A total of 532 dyadic interactions occurred in which one participant could be designated as the winner and the other as the loser. One individual was said to dominate another if it won more than half of the disputes with that individual. The dominance rank of an individual was calculated from the number of birds it dominated within the group, the animal dominating most others having rank number one. The 27 possible combinations for non-sibling dyads resulted in 380 interactions, the nine possible sibling dyads in 152 interactions. A comparison of the mean number of interactions per dyad showed that the birds of the three families interacted as often ($\bar{x} = 16.9$) with siblings as with non-siblings ($\bar{x} = 14.1$) (Mann-Whitney U test, $z = 0.0732$, d.f. = 34, $P = 0.94$). Relatedness was therefore not considered as a factor in the analysis of interaction patterns.

Results

Effect of depressed growth rates on body weight

Body weight differences between the experimental and the control group at the end of the feeding experiment (Table 1) were examined by analysis of variance. In a two-way factorial design the two

Table 1. Mean (± 1 SE) post-fledging body weights of males and females by feeding group: C-birds were raised with food *ad libitum*, E-birds with limited food during the nestling period. $W_{90\%}$ represents the time taken to reach 90% of final weight.

		June		$W_{90\%}$	October		December	
		Mean weight (g)	<i>n</i>	Mean length (days)	Mean weight (g)	<i>n</i>	Mean weight (g)	<i>n</i>
Males	C	471 \pm 4	3	25.5 \pm 1.2	495 \pm 12	3	494 \pm 3	3
	E	417 \pm 9	4	41.8 \pm 1.1	445 \pm 8	4	441 \pm 15	4
Females	C	397 \pm 5	5	26.2 \pm 1.0	424 \pm 7	4	423 \pm 16	4
	E	331 \pm 21	3	38.7 \pm 1.3	400	1	414	1

factors, sex and treatment group, explained 88% of total variance in body weight and each factor had a significant effect when that of the other was controlled for (Table 2). Further, the experimental birds reached 90% of final weight ($W_{90\%}$) at the age of 40.4 (± 1.0 SE) days and the control birds at the age of 25.9 (± 0.7 SE) days. There was no difference between the sexes but the treatment effect (Table 2) was significant.

A large surplus of food was provided to the whole group after the transfer to the outdoor aviary and the body weights were taken again in October and in December (Table 1). The birds of the former E-group were unable to reach a body weight equal to that of the birds of the former C-group. In October and December the differences in body weights between the males of the E-group and the C-group were still significant ($P < 0.05$). For females, there was a significant difference in June. In the autumn a meaningful comparison of female body weights could not be made since two females died accidentally and one escaped, leaving a sample too small for statistical testing.

Effect of depressed growth rates on growth parameters and on linear body size

Analysis of variance of the tarsus growth parameters shows that neither sex nor treatment had a significant effect on the growth constant k . Both factors significantly influenced the asymptote, and explained 68% of its total variance (Tables 3 and 4). Thus, tarsus growth corresponded to model a (Fig. 1); birds growing at depressed rates grew with the same growth constant k towards a lower asymptote.

Each of the two factors, treatment and sex, had a significant effect on final tarsus length when the effect of the other factor was statistically controlled (Table 4). Together they explained 65% of total variance in tarsus length. The age at which 90% of final tarsus length ($T_{90\%}$) was reached was not significantly different for the two sexes, but there was a clear treatment effect (Table 4). The experimental birds reached 90% of final tarsus length at the age of 19.8 (± 0.33 SE) days, the control birds at the age of 17.4 (± 0.30 SE) days.

Table 2. Analysis of variance of final body weights and time taken to reach 90% of final weight.

	Body weight			$W_{90\%}$			d.f.
	SSQ	<i>F</i>	<i>P</i>	SSQ	<i>F</i>	<i>P</i>	
Sources of variance							
Treatment (E/C)	13 068	34.8	<0.001	805.7	157.9	<0.001	1
Sex (male/female)	22 969	61.2	<0.001	3.5	0.7	0.421	1
Interaction Treatment \times sex	109	0.3	0.601	13.9	2.7	0.125	1
Explained	30 511	27.1	<0.001	849.8	55.5	<0.001	3
Total	34 642			911.0			15
% of variance explained by treatment and sex	88.1			91.8			

Table 3. Growth parameter k (mean \pm 1 SE) and asymptote a of the logistic equation, fitted to tarsus of individual chicks, by sex and feeding group: C-birds were raised with food *ad libitum*, E-birds with limited food during the nestling period. $T_{90\%}$ represents the time taken to grow after hatching to 90% of final tarsus length.

		k -value	Asymptote (mm)	n	$T_{90\%}$ (days)	Final tarsus length (mm)
Males	C	0.197 \pm 0.008	70.8 \pm 0.66	4	17.6 \pm 0.42	68.9 \pm 0.56
	E	0.182 \pm 0.008	64.5 \pm 1.24	4	19.7 \pm 0.13	64.3 \pm 1.25
Females	C	0.210 \pm 0.012	65.4 \pm 1.43	5	17.2 \pm 0.43	64.4 \pm 1.06
	E	0.191 \pm 0.012	61.6 \pm 0.32	3	19.1 \pm 0.79	61.6 \pm 0.79

Further, a pairwise comparison of tarsus length within the same family and the same sex also showed that E-birds, at the end of growth, had shorter tarsi than C-birds (Wilcoxon matched-pairs signed-ranks test, $z = 2.02$, $n = 5$, $P = 0.04$). In June and December a pairwise comparison of tarsus length for all birds showed that the tarsus length at fledging represents the final tarsus size of the birds (pairwise t -test, $t = 0.92$, d.f. = 15, $P = 0.374$), i.e. there was no post-fledging tarsus growth.

Effect of depressed growth rates on dominance

Within the same sex all birds of the former C-group had higher ranks than birds of the E-group: males of the C-group had rank number one and two, males of the E-group rank numbers three to six, females of the C-group rank numbers seven and eight, and the female of the E-group rank number nine (Table 5). Within each of the three families a clear dominance hierarchy was found. The males dominated the females and, within the same sex class, the bigger birds dominated the smaller ones. Within the same family and sex class all birds of the former C-group dominated the birds of the

former E-group. An analysis of variance showed that both experimental treatment and sex had significant effects on social rank (Table 6).

Discussion

The present study shows that nestling carrion crows growing at an experimentally lowered growth rate reached a significantly lower final weight much later than did the faster growing nestlings of the control group. Although no curves were fitted to mass gain, for body weight, the growth forms of the two feeding groups conform to model c. In contrast, analysis of growth of linear body dimensions, with tarsus length as the reference, shows that nestlings growing at a depressed rate grow with the same growth constant towards a significantly lower asymptote, and show a significantly shorter final tarsus length. However, these nestlings reached 90% of final tarsus length ($T_{90\%}$) later than the control birds which may indicate that the shape of the growth curves differed, prolonging the latter part of the growth curve in the experimental birds. The main point here is that $T_{90\%}$ changes little compared to that for weight ($W_{90\%}$). An experimental delay of 15 days in

Table 4. Analysis of variance of growth parameters and fledging measurements of tarsus.

	$k \times 100$			Asymptote			Tarsus length			$T_{90\%}$			d.f.
	SSQ	F	P	SSQ	F	P	SSQ	F	P	SSQ	F	P	
Sources of variance													
Treatment (E/C)	12.81	2.80	0.12	99.4	18.3	0.001	61.2	15.5	0.002	23.0	27.3	0.000	1
Sex (male/female)	3.94	0.86	0.37	71.4	13.2	0.003	52.4	13.2	0.003	0.5	0.6	0.438	1
Interaction Treatment \times sex	0.03	0.01	0.94	6.3	1.2	0.302	7.3	1.8	0.200	0.1	0.2	0.682	1
Explained	18.86	1.34	0.30	158.3	9.7	0.002	108.2	9.1	0.002	25.0	9.9	0.001	3
Total	73.73			223.3			155.7			35.1			15
% variance explained by treatment and sex	25.5			68.0			64.8			70.8			

Table 5. Social rank and interactions of experimental and control birds. Indices following the individual indicate the family number.

Individual	sb ₂	dg ₁	ge ₁	bl ₃	db ₂	wh ₂	or ₃	ro ₃	hg ₁
Sex	M	M	M	M	M	M	F	F	F
Treatment group	C	C	E	E	E	E	C	C	E
Rank	1	2	3	4	5	6	7	8	9
<i>Interactions won:</i>									
C versus E within males of family one		45	:	13					
C versus E within males of family two	24		:		0				
	38		:			0			
Total: males versus females			:	137		:		13	
Total: C versus E within sex class	212		:		21		:	41	:
			:				:		0

Table 6. Analysis of variance of social ranks. The interaction between the factors was insignificant ($P = 0.40$) and the data therefore ran as a two-way ANOVA without interactions.

	d.f.	SSQ	F	P
Sources of variance				
Treatment (E/C)	1	12.5	10.71	0.017
Sex (male/female)	1	51.2	43.89	0.001
Error	6	7.0		
$F_{(2,6)} = 22.71, P < 0.002, R^2 = 0.883$				

reaching 90% of final body weight produces a delay of only 2 days in reaching 90% of final tarsus size. Growth forms of linear body size therefore correspond to model a.

In a parallel field study on the carrion crow (Richner, 1989a) the curves for weight gain of chicks in an urban habitat compared to those in a rural habitat followed model c, but tarsus growth, as in the present experimental study, corresponded to model a. Thus, in both the experimental and the field study, birds partly compensated for lowered growth rates by a prolonged phase of weight gain, whereas the growth of skeletal traits showed no significant compensation. Both Ross (1980) in a study on Ipswich sparrows [*Passerculus sandwichensis princeps* (Gunelin)], and O'Connor (1978) on blue tits (*Parus caeruleus* L.), found no correlation between the growth constant k of fledglings and their asymptotic weight. Asymptote variation was reduced by means of a slightly prolonged growth phase. As pointed out by O'Connor (1984) and Ricklefs (cited in Ross, 1980), for body weight, the growth constant k and

the asymptote may represent two independent parameters in the development of individual nestlings, coupled only by the nutritional conditions. Growth of body weight, within the restrictions of weight-size scaling effects, follows model b or c, whereas growth of linear body size follows model a. Since many studies on other species show strong natural selection on linear body dimensions (e.g. Alatalo & Lundberg, 1986; Monaghan & Metcalfe, 1986), this principal difference between growth of body weight and of linear body size should be investigated in a wider range of species. Most studies on nestling growth report increase of body weight only, many include feather growth and few (e.g. Ross, 1980; Murphy, 1983; Richter, 1983; Ricklefs, 1984) describe the growth of linear body structures of permanent character. It is possible that most studies did not find any difference in tarsal lengths under varied breeding conditions because the parents may succeed in maintaining a reduced growth rate of the nestling's body weights above the threshold where effects on fledging body size would become apparent. This could occur especially if strong selection pressures act preferentially on individuals of small body size.

In the field study on carrion crows (Richner, 1989a), the smallest recorded tarsus length of breeding territory holders was 68 mm for males and 65 mm for females. In the present study none of the seven birds from the experimental group reached this size limit, whereas six of nine birds (67%) of the control group reached this limit and thus could potentially acquire a territory and promote their genes into future breeding generations. The field studies on carrion crows also showed that depressed growth rates in an urban habitat resulted in lighter and smaller fledglings,

and social status, access to food and acquisition of a breeding territory were strongly correlated with body size, represented by tarsus length (Richner, 1989a,c). Though body size is correlated with social status, we do not imply that body size itself determines social status. Growth rate depression could affect many other aspects, including neural development, that might not directly be size related. At this point in our understanding, the chick is basically a black box. The results of this and companion studies on carrion crows suggest that selection operates on body size. Early growth in the laboratory influenced body weight, linear size and social status. Low social rank is probably correlated with lower survival rates. Thus, growth rate depression can influence the phenotype sufficiently to affect important life-history parameters.

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