

HABITAT-SPECIFIC GROWTH AND FITNESS IN CARRION CROWS (*CORVUS CORONE CORONE*)

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SUMMARY

(1) The relationship between habitat, chick growth, fledging size and fitness of breeders was studied in two populations of carrion crows, *Corvus corone corone* L., one living in an urban and another in an agricultural environment in south-western Switzerland. The logistic equation was used to model weight gain and tarsus growth, and the growth constant (k) and the asymptote (a) computed, using an iterative least square fitting technique. The chicks in the two habitats are compared with respect to the parameters a and k of the logistic equation. The Darwinian fitness is evaluated for each habitat.

(2) Chicks in the urban habitat gain weight slower, take longer to reach fledging weight and are significantly lighter at fledging than the chicks in the agricultural habitat. Thus, for the weight curves, the chicks in the urban habitat show significantly lower values for both parameters a and k .

(3) Tarsus growth is slower for chicks in the urban habitat, but in contrast to weight gain, growth of tarsus is not prolonged. For tarsus growth the parameter k is identical in the two habitats, but urban chicks show significantly lower values for the parameter a . Tarsus length is fixed by the age of fledging. Chicks in the urban habitat have shorter tarsi at fledging.

(4) Growth of wing is slower in the urban habitat, but, since wing length is incomplete at fledging, no curves were fitted.

(5) Tarsus length of territory-holding adults was measured in both habitats and a critical minimum size for territory acquisition empirically established. Of all fledglings raised in the urban habitat, 79% fall below this critical size and will therefore be unable to acquire a territory and thus be excluded from breeding, whereas only 24% of fledglings raised in the agricultural habitat will be excluded.

(6) Successful parents in the agricultural habitat fledge, on average, 2.7 chicks per year, parents in the urban habitat 1.5 chicks only. 36% of all territory holders in the agricultural habitat fledge young, 39% in the urban habitat. Since a much higher percentage of fledged chicks reach the critical body size in the agricultural habitat, these parents reach a Darwinian fitness five times higher than the parents in the urban habitat.

INTRODUCTION

In this study, I examine the habitat-related variation in nestling growth of carrion crows and its consequences for parental fitness. A link between nestling growth and parent fitness is demonstrated if it can be shown that growth variation can produce non-genetic variation in offspring weight or size, and that differential selection acts on these phenotypes. Many studies document the causes for variation in nestling growth but only a few consider its consequences with respect to natural or sexual selection.

In nature, the growth of nestlings can be affected by: (i) environmental conditions out of parental control; (ii) the age and physical condition of the parents; and (iii) factors which are to a varied degree under parental control, e.g. choice of breeding habitat, hatching date, clutch size, hatching synchrony (for a review, see Ricklefs 1983). Slow growth may modify important life-history attributes of the chicks and thus influence Darwinian fitness of the parents, defined as their contribution of offspring to future breeding generations (Falconer 1981). The life-history attributes which correlate directly with Darwinian fitness of the parents include the probability of post-fledging survival and the probability of becoming a breeder. It is important to consider body weight and linear body size separately, firstly because post-fledging weight is subject to greater change than post-fledging size, and secondly because selection can act independently on weight and on linear body size: post-fledging survival may correlate with fledging weight (Perrins 1965), and mate or territory acquisition with linear body size (Alatalo & Lundberg 1986).

Perrins (1965) showed that the fledgling weight of great tits (*Parus major*) correlates with post-fledging survival and thus demonstrated that variation in fledgling weight, through differential post-fledging mortality, correlates with variation in Darwinian fitness of the parents. Alatalo & Lundberg (1986) have shown that non-genetic phenotypic variation in fledgling tarsus length of pied flycatchers (*Ficedula hypoleuca*), through different probabilities of these phenotypes to become breeders, correlates with Darwinian fitness of the parents. This is to my knowledge the only study on a bird species which demonstrates both that variation in growth produces phenotypic variation in measures of linear body size, and that body size can determine whether a bird will become a breeder.

In the present field study on carrion crows I first look at how the habitat-related variation in the growth dynamics of chicks affects fledging weight and fledging size, and then ask how this variation affects important life-history parameters of the offspring and hence the Darwinian fitness of the parents.

METHODS

The field study was carried out from winter 1985 to spring 1988. One study site was located in agricultural surroundings mixed with forests near St. Saphorin-sur-Morges, in western Switzerland, and the other one in an urban, recreational and parkland habitat in Lausanne, on Lake Geneva.

Crows build a new nest every year in a tree in their territory. All old nests within the two study sites were mapped in February and early March and the site of the new nests, usually built during the second half of March and of April, was recorded. Location and outlay of all territories within the two study sites is known and a large proportion of the territory holders is individually wing-tagged and colour-ringed.

Hatching date was determined by behavioural observation of the male when it was seen for the first time feeding its brood and by climbing the nesting tree at regular intervals. On the first visit after hatching the chicks were individually colour-ringed. In order to prevent excessive heat loss of the chicks, care was taken to inspect the nest only on dry and relatively warm days, especially for the first half of the fledging period. At each subsequent visit to a nest, the number of chicks was recorded, along with the weight, and the length of the tarsus, wing and beak of each chick. Wing length was measured on the flattened wing, and tarsus 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. At the age of 25–30 days the chicks were individually wing-tagged and colour-ringed, and the sex was determined in a laboratory-equipped bus in the field, using the laparoscopy method (H. Richner, unpublished).

Chick growth is described separately for male and female chicks in the agricultural and the urban habitat. Logistic equations of the form

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

were fitted to the weight gain and tarsus growth curves of the chicks. Y refers to a body measurement at age T , k is the rate constant of the logistic equation and b the constant of integration which translates individuals on a common time-scale. Logistic equations of this form produce curves which are symmetric with respect to the point of inflection (I), $y = a/2$. The instantaneous growth rate at age T is given by differentiation of the original equation,

$$dy/dT = ky(1 - y/a).$$

The maximum growth rate (G_{\max}) which occurs at the point of inflection calculates therefore as

$$dy/dT = (ka/2)(1 - a/2a)$$

which reduces to

$$G_{\max} = ka/4.$$

The parameters of the logistic equation were determined using an iterative least-square fitting method. For tarsus growth I fitted a logistic equation to each individual chick. For the increase of body weight I fitted a logistic equation to the entire data set of all chicks of a given sex in each habitat, rather than to each individual chick. As k depends to a certain extent on the quality of fit of the equation to the data, an independent measure, the time taken to grow from 10% to 90% of observed fledging weights ($T_{10-90\%}$), was also considered (Ricklefs 1968).

The weight versus age curves and the size versus age curves for the mean values at age 4, 8, etc. to 32 days are shown in Figs 1–3. Since crows hatch asynchronously and the trees could not be climbed every day, the body measurements for a specified day as shown in Figs 1, 2 and 3, were found by interpolation between two original data points. Fledgling weights, sizes and growth parameters are given in Tables 1 and 2. Unless otherwise indicated, all significance values throughout the paper are two-tailed.

A sample of 430 crows was caught in a large trap between 1985 and 1988. All birds were measured, individually marked, their sex determined by the laparoscopy method and their age determined by inspecting the arrangements of feather-marks (Svensson 1984). This sample demonstrated that the tarsus length of juveniles in their first winter after fledging is highly correlated (Table 3) with other body measurements, and hence it was taken as a measurement representative of overall body size. A sample of forty-two crows which were captured as juveniles or fledglings, and recaptured and measured at least 9 months and at most 30 months after the initial capture, demonstrated that tarsus length is constant over time (Fig. 4). The maximum change over this time interval was 1 mm, which falls within the rounding error.

A sample of forty-nine adult territory-holding crows was caught in order to determine the mean and minimum body size (=critical size) of territory holders. These crows were caught in their territory using a stupefying bait (alpha-Chloralose or Avertin).

TABLE 1. Fledgling body weight (± 1 S.D.) and growth parameters (± 1 S.D.) by sex and breeding habitat. K = growth constant of the logistic equation, fitted to the entire dataset of each group, $T_{10-90\%}$ = time taken to grow from 10% to 90% of fledgling body weight, G_{\max} = maximum growth rate, at point of inflexion of the logistic curve

Habitat	Body weight			Growth parameters				
	\bar{x}	n	P	k	n	P	$T_{10-90\%}$ (days)	G_{\max} (g d ⁻¹)
Males								
Agricultural	443 \pm 53	24	<0.001	0.355 \pm 0.007	17	<0.001	16	36.9
Urban	389 \pm 38	24		0.267 \pm 0.009	16		18	24.1
Females								
Agricultural	392 \pm 29	21	<0.001	0.358 \pm 0.007	13	<0.001	15	33.4
Urban	326 \pm 44	27		0.248 \pm 0.013	14		17	18.1

A nest was considered successful if at least one chick fledged. Habitat-specific fitness, for each of the study sites, was calculated by first multiplying the mean number of fledged nestlings for successful nests by the proportion of territories of the total from which young fledged, and then multiplying this number by the proportion of nestlings above the critical tarsus size.

RESULTS

Hatching date

As hatching date is shown in many studies to influence growth of chicks and weight of fledglings, it is analysed here with respect to the two habitats and to yearly differences. Median hatching date was not significantly different between the 4 years ($P > 0.3$) and data were therefore pooled for each habitat. Median hatching date was 5 May in the agricultural habitat and 3 May in the urban habitat. The difference is not significant (median test, $\chi^2_{147} = 1.02$, $P > 0.3$).

Chick growth variation

Weight gain

Weight differences between the sexes are not significantly different before the age of 20 days (Mann-Whitney U -test, $z = 2.23$, $n = 26$, $P = 0.03$) in the agricultural habitat, and not before the age of 24 days ($z = 2.37$, $n = 22$, $P = 0.02$) in the urban habitat, but are significant thereafter. In each habitat the sexes do not differ significantly in their k value. Thus, males and females in the same habitat reach their respective asymptotes at the same age.

The chicks in the urban habitat gain weight slower than the chicks in the agricultural habitat (Fig. 1), as shown by the following.

(a) Lower maximum growth rates (G_{\max}) (Table 1).

(b) Significant weight differences between males in the two habitats at the age of 8 days (Mann-Whitney U -test, $z = 3.36$, $n = 29$, $P < 0.001$) and thereafter. Females in the urban habitat are significantly lighter than females in the agricultural habitat from the age of 8 days ($z = 2.84$, $n = 21$, $P < 0.001$) and thereafter (Fig. 1).

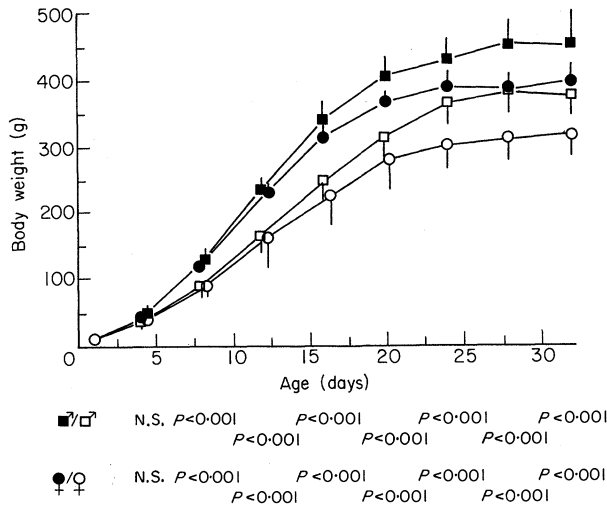


FIG. 1. Mean body weight ($\pm 95\%$ C.L.) of nestlings in relation to age. Symbols indicate (■) males ($n = 11-17$) and (●) females ($n = 12-18$) in the agricultural habitat, and (□) males ($n = 12-17$) and (○) females ($n = 11-15$) in the urban habitat. For graphical clarity, the confidence limits are shown on one side of the mean only. Given below, at 4-day intervals, are significance values for differences in male weight between the two habitats, and for differences in female weight between the habitats.

(c) The growth constant k of the logistic equation is significantly lower for urban chicks, i.e. they reach their respective asymptotes significantly later than rural chicks (Table 1).

(d) Chicks in the agricultural habitat took a mean of 15.5 days to grow from 10% to 90% of fledging weight, whereas the urban chicks took a mean of 17.5 days.

TABLE 2. Fledgling tarsus length (± 1 S.D.) and growth parameters (± 1 S.D.) by sex and breeding habitat. K = mean value for the growth constant of the logistic equation, fitted to individual chicks, G_{\max} = maximum growth rate, at point of inflexion of logistic curve

Habitat	Tarsus length			Growth parameters				
	\bar{x}	P	n	k	n	P	G_{\max} (mm/d ⁻¹)	P
Males								
Agricultural	70.0 ± 2.4	< 0.001	24	0.213 ± 0.019	17	N.S.	3.82	< 0.001
Urban	65.8 ± 1.4		24	0.208 ± 0.019	16		3.45	
Females								
Agricultural	66.0 ± 2.1	< 0.005	21	0.218 ± 0.021	13	N.S.	3.68	< 0.001
Urban	60.5 ± 4.0		27	0.211 ± 0.012	14		3.25	

TABLE 3. Correlation matrix (Pearsons product-moment correlation) for different morphological traits of (a) juvenile males and (b) juvenile females. Sample sizes are given in brackets, significance values are one-tailed

	Weight	Tarsus length	Wing length	Beak length	Beak gape	Beak height
(a)						
Tarsus length	0.628 (170) $P < 0.001$					
Wing length	0.574 (169) $P < 0.001$	0.811 (169) $P < 0.001$				
Beak length	0.438 (169) $P < 0.001$	0.160 (169) $P = 0.019$	0.084 (168) $P = 0.139$			
Beak gape	0.515 (166) $P < 0.001$	0.465 (166) $P < 0.001$	0.426 (165) $P < 0.001$	0.614 (166) $P < 0.001$		
Beak height	0.443 (131) $P < 0.001$	0.233 (131) $P = 0.004$	0.340 (130) $P < 0.001$	0.357 (131) $P < 0.001$	0.268 (131) $P = 0.001$	
Sternum length	0.423 (23) $P = 0.023$	0.605 (23) $P = 0.001$	0.403 (23) $P = 0.030$	0.205 (22) $P = 0.183$	0.588 (22) $P = 0.002$	0.232 (22) $P = 0.153$
(b)						
Tarsus length	0.615 (146) $P < 0.001$					
Wing length	0.467 (144) $P < 0.001$	0.682 (144) $P < 0.001$				
Beak length	0.471 (146) $P < 0.001$	0.414 (146) $P < 0.001$	0.272s (144) $P < 0.001$			
Beak gape	0.373 (142) $P < 0.001$	0.462 (142) $P < 0.001$	0.396 (140) $P < 0.001$	0.700 (142) $P < 0.001$		
Beak height	0.417 (113) $P < 0.001$	0.183 (113) $P = 0.026$	0.227 (111) $P = 0.008$	0.460 (113) $P < 0.001$	0.351 (113) $P < 0.001$	0.228 (113) $P = 0.008$

Tarsus growth

Growth differences between the sex-classes within the same habitat are small. In each habitat the size difference between the males and females is not significant before the age of 16 days. At the age of 16 days the sexes differ at a significance level of 5%, and at less than 1% thereafter. *K*-values are not significantly different between males and females in the same habitat. Although the sexes grow towards different asymptotes, they reach the asymptote at the same age. In both habitats maximum growth rates, which occur at the point of inflection, are not significantly different between males and females.

Within the same sex-class, the tarsus of chicks in the urban habitat grows slower than the tarsus of chicks in the agricultural habitat (Fig. 2). This is seen by:

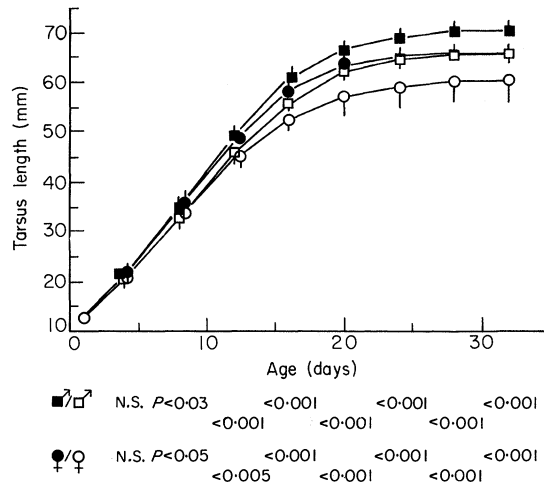


FIG. 2. Mean tarsus length ($\pm 95\%$ C.L.) of nestlings in relation to age. Symbols indicate (■) males ($n=11-17$) and (●) females ($n=12-18$) in the agricultural habitat, and (□) males ($n=12-17$) and (○) females ($n=11-15$) in the urban habitat. For graphical clarity, the confidence limits are shown on one side of the mean only. Given below, at 4-day intervals, are significance values for differences in male tarsus length between the two habitats and, for differences in female tarsus length between the habitats.

(a) the smaller maximum growth rates (G_{\max}) for males and females in the urban habitat (Table 2) if compared within the same sex-class to the chicks in the agricultural habitat (t -test; males: $t_{27}=3.92$, $P=0.001$; females: $t_{25}=3.57$, $P=0.001$);

(b) the significant differences in tarsus length between the two habitats. At the age of 4 days mean tarsal lengths of males do not differ significantly between the two habitats, at the age of 8 days the differences are significant at the 5% level (Mann-Whitney U -test, $z_{27}=2.13$, $P=0.03$) and highly significant thereafter ($z_{26}=3.91$, $P<0.001$). Similar differences are observed for the females in the two habitats (day 8: $z_{22}=1.96$, $P=0.05$; day 16: $z_{21}=3.47$, $P<0.001$) (Fig. 2).

However, within each sex-class the growth constant k of the logistic equation is not significantly different between the two habitats (Table 2). Thus, the chicks in the urban habitat reach their respective asymptotes as fast as chicks in the agricultural habitat.

Wing growth

Wing growth from hatching to fledging is not significantly different between males and females in the same habitat and data were therefore pooled. Between the habitats, however, the differences are significant at the age of 8 days and thereafter (Fig. 3). Here too, the birds in the urban habitat grow slower than the rural birds. I did not fit a logistic curve to the data since, as k depends very much on the asymptote and the wing length of fledglings is well below the final wing length, little confidence could be attached to an estimated growth constant.

Variation in fledgling size, weight and number

Fledgling size and weight were analysed in relation to the breeding habitat and the sex of the chicks (Tables 1 and 2). At fledging, the males were significantly heavier (t -test,

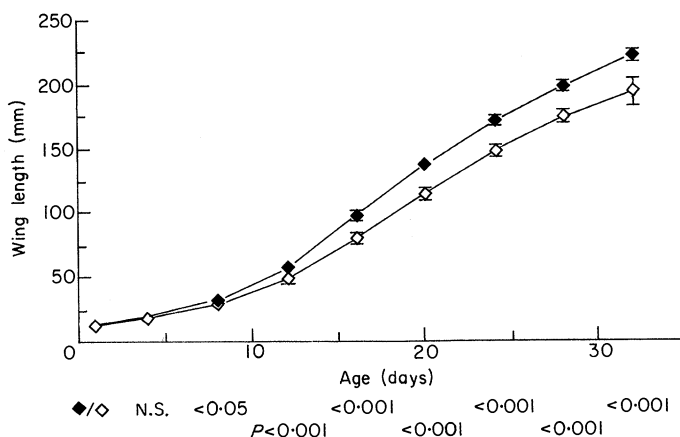


FIG. 3. Mean wing length ($\pm 95\%$ C.L.) of nestlings in relation to age. Symbols indicate (\blacklozenge) chicks in the agricultural habitat ($n = 23-35$) and (\diamond) chicks in the urban habitat ($n = 23-32$). Given below, at 4-day intervals, are significance values for differences in pooled male and female wing length between the two habitats.

$t_{94} = 5.76$, $P < 0.001$) and bigger ($t_{82.2} = 6.74$, $P < 0.001$) than the females and the two sexes are therefore analysed separately.

By the age of fledging, the males in the urban habitat were both significantly lighter ($t_{46} = 4.01$, $P < 0.001$) and smaller ($t_{37.9} = 7.45$, $P < 0.001$) than the males in the agricultural habitat and the females in the urban habitat lighter ($t_{44.8} = 6.24$, $P < 0.001$) and smaller ($t_{40.9} = 6.11$, $P < 0.001$) than the females in the agricultural habitat.

For the calculation of breeding success only nests where at least one chick fledged are included. In the agricultural habitat a mean (± 1 S.E.) of 2.68 ± 0.24 chicks fledged per nest, whereas in the urban habitat only 1.54 ± 0.14 chicks fledged. The difference is highly significant ($t_{42} = 4.21$, $P < 0.001$).

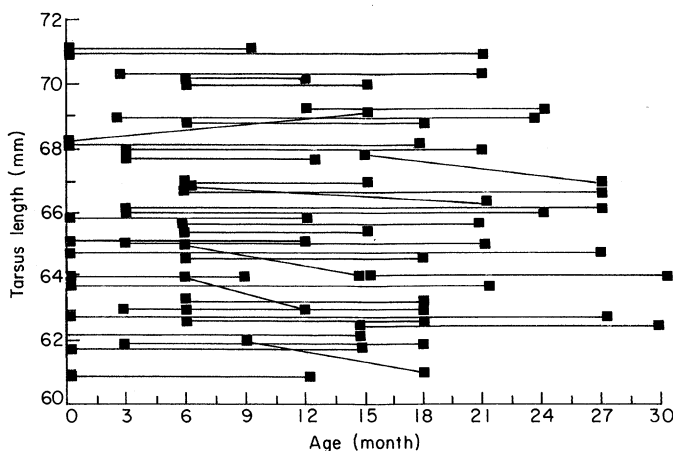


FIG. 4. Tarsus lengths of forty-two carrion crows of known age at their first capture and at their last recapture.

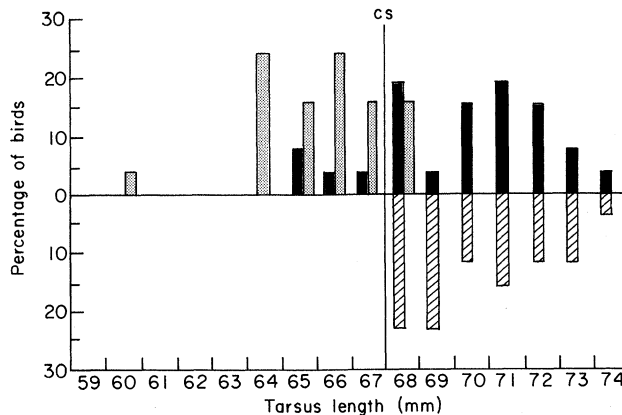


FIG. 5. Percentage distribution of male birds by tarsus length for: breeders (■) ($n=28$), fledglings in the agricultural habitat (■) ($n=24$) and fledglings in the urban habitat (▨) ($n=24$). The vertical line shows the minimum tarsus length of breeders (cs = critical tarsus size for territory acquisition).

Body size, resource-holding potential and fitness

Finally, the question of most interest is whether small fledgling size, as observed for most urban chicks, affects lifetime parameters, such as survival or reproduction. Carrion crows are territorial and a territory is a prerequisite for reproduction. In both study sites there are large non-breeder flocks with a high proportion of adult birds. Much fighting occurs between territorial and non-territorial birds. Territories can therefore be viewed as a limited resource which can only be acquired by few birds. Two marked territory-holding adults, one in each habitat, disappeared between 1985 and 1987, and it is therefore assumed that predation on adults is not different in the two habitats. The aim of this section is, as a first step, to look at the body size of established territory holders, i.e. birds which are known to have reproduced successfully and thus to own a suitable territory for

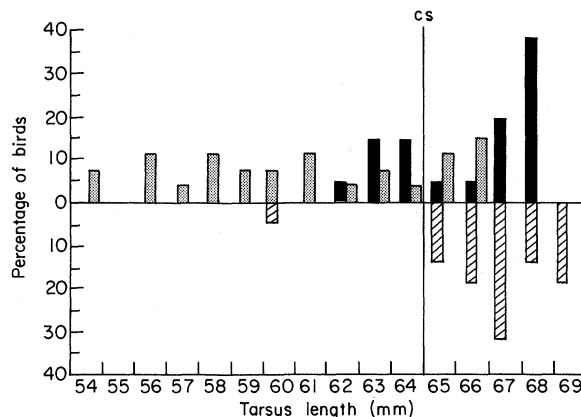


FIG. 6. Percentage distribution of female birds by tarsus length for: breeders (■) ($n=21$), fledglings in the agricultural habitat (■) ($n=21$) and fledglings in the urban habitat (▨) ($n=27$). The vertical line shows the minimum tarsus length of breeders (cs = critical tarsus size for territory acquisition).

reproduction, in order to determine empirically the critical minimum size necessary for acquiring the limited resource. Then, as a second step, this critical size is compared to the size of fledglings raised in the agricultural and in the urban habitat.

The weight and wing length of a bird can change with age or season, while weight can also change with social status, but tarsus length does not change after fledging. This assumption was tested on a sample of forty-two crows which were initially caught as juveniles or fledglings and then repeatedly caught over a period of up to 2.5 years (Fig. 4). There was no significant difference in tarsus size between the first capture and consecutive recaptures of these birds (t -test for paired samples, $t_{40}=1.67$, $P>0.1$), nor was there a trend for the tarsus to grow with age. The maximum change in tarsus length was 1 mm, which falls within the rounding error, as measures were rounded to the nearest millimetre.

The mean (± 1 S.E.) tarsus length of urban male territory owners is 70.12 mm (± 0.52 , $n=16$) as compared to that of rural male territory owners of 70.42 mm (± 0.43 , $n=12$). The difference is not significant ($t_{26}=0.41$, $P=0.67$) and data from both habitats were therefore pooled. The smallest recorded tarsus in a breeder measured 68 mm in both habitats. Similarly, there was no significant difference between urban ($\bar{x}=66.2$ mm, ± 0.80 , $n=10$) and rural ($\bar{x}=67.0$ mm, ± 0.38 , $n=11$) females ($t_{13}=0.90$, $P=0.38$). The observed difference of 0.8 mm between urban and rural females is mainly due to one female with a tarsus of only 60 mm. This bird failed repeatedly in 1986, 1987 and 1988 to breed successfully. Excluding this bird yields a minimum tarsal length of 65 mm for territory-owning females.

The frequency distributions of male and female territory-owners in relation to tarsus size are shown in Figs 5 and 6. Added are the observed values for the fledglings in the agricultural and urban habitats: 84% of the male fledglings raised in the urban habitat do not reach the critical size (68 mm) for territory acquisition, whereas only 14% of the male fledglings from the countryside do not reach this size. Similarly, 74% of the urban female fledglings fall below the critical size for females (65 mm) compared to only 33% for rural females. Assuming equal sex ratios at fledging, 79% of all fledglings raised in the urban habitat will be excluded from future breeding as compared to 24% of all fledglings raised in the agricultural habitat.

For the calculation of fitness in relation to habitat, all territory-holding pairs were considered, including those that failed in their breeding attempt, i.e. did not produce any young which fledged. The proportion of successfully reproducing territory holders of the total number of territory holders thus represents the probability that a pair succeeds in their breeding in a specified habitat. This probability multiplied by the mean number of young per successful pair gives the mean number of young produced per territory-holding pair. In the agricultural habitat 36% of all territory-holding pairs fledged a mean of 2.68 young compared to 39% of all urban territory holders, who fledged a mean of 1.54 young. The mean number of fledged young per territory-holding pair in the agricultural habitat is therefore $0.36 \times 2.68 = 0.96$, and in the urban habitat $0.39 \times 1.54 = 0.60$.

Based on these figures, the net production of potential breeders in the countryside, with a mean of 0.96 chicks per territory holding pair, and a probability of 79% that these chicks will become breeders, is $0.96 \times 0.79 = 0.76$. In the urban habitat, where the mean is 0.60 chicks per territory holding pair, with a probability of 24% that these chicks will become breeders, the figure calculates as $0.60 \times 0.24 = 0.14$. Therefore, assuming equal reproductive life-spans, similar post-fledging mortality and similar adult predation in the two habitats, the maximum achievable fitness for breeders, in terms of their contribution

of offspring to future breeding generations (Falconer 1981), is more than five times higher in the agricultural habitat than in the urban habitat.

DISCUSSION

Many studies on passerines show that a number of morphological characters are heritable to varied degrees (Smith & Zach 1979; Smith & Dhondt 1980; Ricklefs & Peters 1981; Dhondt 1982; Boag 1983; Grant 1983; Ricklefs 1984). However, behavioural and physical characteristics of the parents, and environmental or habitat-related factors can modify the offspring's phenotype sufficiently to affect important life-history parameters, e.g. juvenile survival, the potential for mate acquisition and for breeding, social status, or habitat selection (Lundberg *et al.* 1981). The influence of a nestling's growth dynamics on fledging size is important if selection acts on morphological traits which are fixed at the end of the nestling period. In this study, lower daily weight gain affected tarsus size, with slow-growing birds in the urban habitat reaching a lower asymptote. Natural selection, measured by the potential for territory acquisition was, at least in males, clearly influenced by tarsus size. Small birds are excluded from territory acquisition and hence from reproduction. Alatalo & Lundberg (1986) showed that in breeding pied flycatchers (*Ficedula hypoleuca* Pall.) an environmental deviation due to food factors affects tarsus length of chicks. Furthermore, there was stabilizing selection on tarsus length for survival and male mating success. Selander (1965) presents evidence that in male great-tailed grackles (*Quiscalus mexicanus* Gmelin), body size is set by a balance between sexual selection favouring increased size in the breeding season, and selection for survival favouring decreased size. Although there may be some general trends, the target and direction of selection pressures is probably to a large extent species-specific. To demonstrate a clear relationship between chick growth and natural or sexual selection, there must be sufficient evidence showing that body size at the end of the fledging period correlates with adult body size. That is, there is either no post-fledging growth or, at least, proportional growth of a given morphological trait amongst individuals. Is there such evidence?

As this question may have different answers for different morphological traits, I will consider tarsus, wing and beak separately. As shown here, in carrion crows the tarsus length achieved at fledging remains unaltered for the rest of a bird's life. This seems to be the general case for Passerines, although Woolfenden (1978) found some additional tarsus growth of Florida scrub jays (*Aphelocoma coerulescens* Bosc) during the first and second year of life. Unfortunately, there is no indication whether this observed 'catch-up'-growth of the Florida scrub jays occurs mainly in individuals which are small in relation to their true genotype. Catch-up growth, also termed compensatory growth, has been reported for some mammals (Tanner 1963; Williams & Hughes 1975). In contrast to tarsal length, the wing length may change with each moult and therefore be less directly affected by the rearing conditions. Furthermore, the wings are subject to wear which may introduce a source of variation that masks phenotypic differences between individuals. Beak length, in the present study, varied up to 3 mm between recaptures of the same individual. In male parent rooks (*Corvus frugilegus* L.) beak length decreased significantly during the breeding season (Green 1981), whereas in females it increased during incubation; tarsus and wing length showed no significant trend. In rooks beak length seemed to vary with the extent of wear, which may be extreme during breeding, when there is a peak demand for feeding. In Darwin's medium ground finches (*Geospiza*

fortis L.) beak length between recaptures of the same individuals varied in some years, but not in others (Price & Grant 1984). The current literature thus suggests that there are species-specific differences in post-fledging growth of these characters. In summary, carrion crows show high variation in weight, wing and beak length of individuals between first and subsequent captures, but there was no significant increase or decrease in tarsus length over time (Fig. 4).

Although this study deals with the effect of reduced growth on phenotypic traits and not with the causes of reduced growth, I would nevertheless like to consider the following hypotheses for the causes of the differential growth dynamics of the chicks in the two habitats.

(a) Do the breeding parents in the urban habitat differ in genotype from the breeders in the agricultural habitat? For all phenotypic attributes which were measured on adults of the breeding population, there was no significant difference detectable between birds in the two habitats. Assuming that, for breeders, the phenotype is a reliable representation of the genotype, there is no support for this hypothesis.

(b) Could differences in egg size give rise to smaller fledglings in the urban habitat? Egg size was not measured to avoid disturbing the breeding female, which may abandon its clutch early in the breeding cycle. Rofstad & Sandvik (1985), in hooded crows (*Corvus corone cornix* L.), found no significant difference in egg size from one year to another, nor between different-sized clutches or different laying dates. A decrease in egg volume was observed with increasing laying order. Rofstad & Sandvik (1987), in hooded crows, show high positive correlations of the egg volume with hatchling body weight, wing, bill, toe, and claw lengths, but not with hatchling tarsus length. Schifferli (1973) showed that hatching weight in great tits (*Parus major* L.) is positively correlated with egg weight, but the nestling weight close to fledging is not correlated with egg weight or hatching weight. No logistic curves were fitted in his study, but it is shown that age of maximum weight is not significantly correlated with egg weight. This seems to indicate that, in great tits, chicks from small and large eggs grow equally fast and, if curves were fitted, would have identical *k*-values. As Ricklefs (1984) pointed out, there are virtually no studies which show that initially bigger hatchlings grow faster. In the present study, it is unlikely that the difference in growth and body size of chicks in the two habitats is attributable to differences in egg size.

(c) Are the breeders in the agricultural habitat older or more experienced? In a study on red-winged (*Agelaius phoeniceus* L.) and yellow-headed (*Xanthocephalus xanthocephalus* Bonaparte) blackbirds, Crawford (1977) found that yearling parents raised lighter nestlings than did older birds. In contrast, yearling Ipswich sparrows (*Passerculus sandwichensis princeps* L.) in Ross' study (1980) produced heavier fledglings than older adults. In the present study on carrion crows, there is no evidence that older or more experienced birds would preferentially breed in the habitat of higher breeding success. Territory holders were observed to breed each year in the same territory. Such a long-term territorial system, as is typical for the carrion crow, leads to a stable mixture of older and younger breeders in each of the two habitats.

(d) Do food factors differ between the two habitats and reduce instantaneous growth rates and fledgling size in the urban habitat? Yom-Tov (1974) performed an experiment in which food abundance was increased in some territories of carrion crows. The fledging chicks in his experimental group were significantly heavier than controls without additional food. Yom-Tov does not report an effect on tarsus length: either it did not occur or it was not measured. Concerning this study, the observed slower growth and

smaller fledgling tarsus length in the urban habitat is most probably caused by poor feeding conditions.

(e) Could thermal consequences of larger brood sizes in the agricultural habitat lead to more intensive tarsus growth and thus affect its final length? As heat loss depends on the volume-to-surface ratio, the chicks in larger broods may be at a thermal advantage and this may influence the rate of bone growth. Brookes & May (1972) showed that the prenatal development of humerus, radius, femur and tibia vary linearly with the temperature of the chick embryo. However, there is no study which shows post-natal temperature-dependent bone growth. To evaluate the hypothesis of temperature, and hence brood-size dependent tarsus growth, I compared tarsal length of fledglings from identical brood sizes among the habitats. For broods of two, three and four chicks 10–20 days after hatching, both tarsal length ($P < 0.005$, two-way factorial ANOVA, controlling for sex) and body weight ($P < 0.02$) at fledging were significantly lower in the urban habitat than in the agricultural habitat. Thus, there is no evidence to explain the observed body size differences between the habitats by the thermal consequences of larger brood sizes in the agricultural habitat.

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